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Soybean tolerance to soybean cyst nematode (Heterodera glycines Ichinohe), and interactions between H glycines and Phialophora gregata, the causal agent of brown stem rot of soybean

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Soybean tolerance to soybean cyst nematode *(Heterodera glycines* Ichinohe), and interactions between *H. glycines* and *Phialophora gregata*, the causal agent of brown stem rot of soybean

by

James Edward Behm

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For the Major Program

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For the Graduate College

To my family, friends, and co-workers

for your assistance, support, and encouragement.

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ABSTRACT

Experiments were conducted in *Heterodera glycines*-infested and noninfested fields in 1994, 1995, and 1996 to evaluate *H. glycines*-susceptible soybean genotypes for tolerance to *H. glycines*, the soybean cyst nematode. Results of linear regression analysis of relative yield [RY=(individual plot yield÷experiment mean yield)×100] versus $\log_{10}$-transformed initial *H. glycines* soil egg population densities [Log_{10}(Pi+1)] revealed significant inverse relationships for all genotypes evaluated, including *H. glycines*-resistant 'Jack'. Regression slope values were used as indicators of tolerance, and regression Y intercepts were used as indicators of relative yield potential in absence of the nematode. Tolerance indices [TI=(mean RY in infested fields÷mean RY in noninfested fields)×100]) also were calculated for each genotype and correlated well with values for linear regression slopes of RY versus Log_{10}(Pi+1). Selected genotypes were grown in growth chamber experiments in soil infested with increasing *H. glycines* egg population densities. Significant inverse linear relationships between plant growth and initial egg inoculum densities were detected for all genotypes evaluated, but tolerance assessment in the growth chamber was poorly correlated with that from field evaluations.

Greenhouse and growth chamber experiments were conducted to determine the effects of *H. glycines* and *Phialophora gregata*, the brown stem rot pathogen, on each other and on soybean growth. Incidence and severity of stem discoloration characteristic of *P. gregata* infection of *H. glycines*-susceptible but not PI 88.788-

derived *H. glycines*-resistant, genotypes was greater in potting mix infested with both pathogens than in potting mix infested with *P. gregata* alone, regardless of genotype reaction to *P. gregata*. A similar increase in stem discoloration was detected in a 'Peking'-derived *H. glycines* resistant, *P. gregata*-susceptible but not a 'Peking'-derived *H. glycines* resistant, *P. gregata*-resistant, genotype. When each pathogen was inoculated on separate half-root systems of split-root plants, incidence of stem discoloration was intermediate to, but not different from, incidence when *H. glycines* and *P. gregata* were inoculated on the same half-root system or when half-roots were inoculated with *P. gregata* alone. No effect of *P. gregata* on total *H. glycines* reproduction was detected in any experiment.

GENERAL INTRODUCTION

Introduction

Historical perspective

The soybean cyst nematode, *Heterodera glycines* Ichinohe, is a major pathogen of soybean (*Glycine max* (L.) Merrill) and is known to infest soil throughout most soybean-producing regions of the world (Niblack, 1993). The nematode first was described in 1915 in Japan (Hori, 1915), however, symptoms of *H. glycines* damage to soybean were observed in Japan for many years prior to 1915 and in China for centuries (Noel, 1992). Following its first reported occurrence in the United States in 1954 in North Carolina (Winstead et al., 1955), *H. glycines* has become the most damaging pathogen of soybean in the United States (Doupnik, 1993; Wrather et al., 1995). The nematode likely was introduced into the United States in shipments of ornamental flower bulbs imported from Japan or in soil imported from Asia for the purpose of obtaining *Bradyrhizobium japonicum* (Kirchner) Buchanan cultures (Noel, 1992). *Heterodera glycines* is now widely distributed throughout the northcentral United States (Workneh et al., 1996). In 1978, *H. glycines* was identified in Winnebago County, Iowa (Tylka, 1995), and it is currently known to be present in more than 75% of Iowa counties.

Biology, pathology, and management of *H. glycines*

Heterodera glycines begins its life cycle as eggs, and after an initial molt within the egg shell, the nematodes hatch as vermiform second-stage juveniles (J2); the J2 are the only infective stage of the nematode. Hatched J2 penetrate soybean roots, migrate intracellularly through cortical tissue to the periphery of the stele, and induce formation of specialized feeding cells, called syncytia, by injecting secretions into the root cells (Endo, 1987). During development, the nematodes molt three additional times, and, eventually, sexual differentiation of adult males and females occurs.

At the final molt to the adult stage, males revert to a vermiform shape, cease feeding, and exit the roots, whereas females continue feeding, swell to a lemon shape, and, eventually, rupture the root epidermis and protrude through the root surface. Males are attracted to females by a pheromone (Rende et al., 1982), and mating occurs. Fertilized females deposit eggs both externally within a gelatinous matrix and internally. When egg laying is completed, the females die and the bodies of dead females, referred to as cysts, eventually become dislodged from the roots (Agrios, 1988; Sinclair, 1989). Each female can produce as many as 600 eggs (Young, 1992), and, under optimum conditions, *H. glycines* can complete a life cycle in 24 days, allowing several generations to be produced in a single growing season (Lauritis et al., 1983).

Eggs contained within the external gelatinous matrix hatch readily and serve as secondary inoculum within a crop season, whereas eggs contained within the cyst hatch more slowly due to inhibitory compounds associated with the body wall of the cyst (Ishibashi et al., 1973; Okada, 1972). Dormancy can be induced by declining soil

temperatures late in the growing season (Hill and Schmitt, 1989; Ross, 1963), and eggs contained within cysts can remain viable in soil for 11 years or longer (Inagaki and Tsutsumi, 1971). Eggs contained within cysts are the long-term survival stage of the nematode.

Soybean plants infected with *H. glycines* typically exhibit stunting and chlorosis. These symptoms are caused, in part, by reduced ability of infected roots to translocate water and nutrients upward due to physical damage from syncytial and nematode development (Radcliffe et al., 1990). However, research results of Heatherly et al. (1992) indicate that yield suppression due to *H. glycines* parasitism results from more than just reduced translocation. Infection of soybean roots by *H. glycines* also can reduce formation and efficiency of nitrogen-fixing nodules (Barker et al., 1972; Huang et al., 1984; Ko et al., 1986). Above-ground symptoms of *H. glycines* infection within a field often occur in oval patches elongated in the direction of tillage and may range from nonexistent to so severe as to cause plant death. Stunting and chlorosis caused by *H. glycines* often are attributed as symptoms associated with other diseases or with environmental stresses (Edwards, 1986; Epps, 1971; Sinclair, 1989; Tylka, 1995). Consequently, accurate field identification of *H. glycines* only can be accomplished by observation of females and cysts attached to the roots of soybean plants that have been carefully removed from the soil. *Heterodera glycines* soil population densities can increase to damaging levels in any soil type, but yield loss tends to be greater in sandy soil where the soybean crop is subjected to periodic moisture stress and nutrient deficiencies. Yield loss due to *H. glycines* can range from slight to 90% and, thus,

represents a serious threat to soybean production (Niblack et al., 1992; Sinclair, 1989).

Movement of infested soil is the predominant means of dispersal of the nematode. *Heterodera glycines* eggs and cysts are non-motile, and the J2 can move only centimeters, however, anything that moves soil can disperse *H. glycines* eggs, cysts, and J2 with the soil. Infested soil can be transported by wind, water, livestock, machinery, and wildlife (Edwards, 1986; Epps, 1971; Sinclair, 1989; Tylka, 1995). The nematode also can be dispersed in peds of infested soil in improperly cleaned seedstock (Epps, 1969).

Management of *H. glycines* is achieved through a combination of several strategies including cultural practices that maintain sufficient levels of plant health to maximize yields and management of soil movement to reduce local spread of the nematode (Tylka, 1995). Chemical control with nematicides has not proven to be useful due to lack of consistent effectiveness (Epps and Young, 1981; Reese et al., 1988; Weaver et al., 1985) as well as economic and environmental considerations.

Heterodera glycines is most effectively managed by rotation of nonhost crops and *H. glycines*-resistant soybean cultivars. However, limitations to this strategy exist. In Iowa and most of the upper Midwest, corn (*Zea mays* L.) is the most commonly grown nonhost crop, and many producers utilize a two-year corn-soybean rotation in most fields. In Midwest fields infested with *H. glycines*, this rotation is ineffective at reducing population densities of the nematode to below damaging levels. Soybean cultivars resistant to *H. glycines* are widely available (Munkvold et al., 1996), and these cultivars restrict reproduction of the nematode. However, individual nematodes capable

of reproducing on resistant cultivars are present in most *H. glycines* populations (Anand et al., 1994; Triantaphyllou, 1975; Young, 1982). Use of the same source of resistance each time *H. glycines*-resistant cultivars are grown may increase the proportion of nematodes in a population capable of reproducing on those cultivars, resulting in a gradual genetic shift, referred to as a race shift, in the nematode population. Alternating among sources of resistance in *H. glycines*-resistant cultivars may reduce or counter selection pressure exerted on a nematode population by a single resistance source (Luedders and Dropkin, 1983; Young, 1994). Unfortunately, most of the *H. glycines*-resistant cultivars currently available to Iowa soybean producers have resistance derived from a single source, PI 88.788 (Munkvold et al., 1996). Current Iowa State University management recommendations include growing a *H. glycines*-susceptible cultivar every second or third time soybean is grown in infested fields to offset selection pressure occurring when *H. glycines*-resistant cultivars are grown (Tylka, 1995). This tactic may avoid or delay shifts in avirulence gene frequencies within a nematode population (Triantaphyllou, 1975; Young and Hartwig, 1988), although, results of some research suggest it is unlikely to shift a nematode population to a less virulent genetic composition (Anand et al., 1995). Additionally, *H. glycines*-susceptible soybean cultivars differ in amount of yield loss when parasitized by similar numbers of nematodes (Hussey and Boerma, 1992).

Soybean tolerance to *H. glycines*

The ability of a plant to maintain its growth and yield while supporting development and reproduction of a nematode population is a characteristic known as

tolerance (Dropkin, 1955). Cook and Evans (1987) suggested that tolerance and resistance function independently of each other and that tolerance refers to the amount of host injury (i.e. yield loss) caused by nematode activity, whereas resistance defines the host plant's ability to restrict nematode reproduction. Thus, a nematode-susceptible cultivar may be tolerant to nematode attack, whereas a nematode-resistant cultivar may be intolerant (Hussey and Boerma, 1992). Resistance to nematodes is genetically controlled, and the usual mechanism for resistance is one of several forms of hypersensitive response (Kim et al., 1987).

Knowledge of the inheritance and mechanisms of tolerance to nematode attack is less clearly understood. Wallace (1987) suggested that tolerance to nematodes is a function of several physiological and morphological plant characteristics, although the effect of one single trait may predominate. Wallace further stated that plants tolerant to abiotic and biotic stresses (i.e. drought tolerance) may be tolerant to nematodes that cause similar stresses. Other researchers (Cook and Evans, 1987; Evans and Franco, 1979) suggested that tolerance to nematode attack may be affected by interactions with other stresses. Additionally, greater water use efficiency has been proposed as a contributing factor to tolerance (Evans and Haydock, 1990).

Tolerance to nematode parasitism has been demonstrated and utilized in the production and breeding of coffee (*Coffea arabica* L.) (Zhang and Schmitt, 1995), cotton (*Gossypium hirsutum* L.) (Bowman and Schmitt, 1994), oat (*Avena sativa* L.) (Radewald et al., 1971), soybean (Nyczepir and Lewis, 1979), and sugar beet (*Beta vulgaris* L.) (Hiejbroek et al., 1977). Most nematode tolerance research has been

conducted with the potato cyst nematodes (*Globodera rostochiensis* Wollenweber and *G. pallida* Stone) and potato (*Solanum tuberosum* L.). Trudgill and Cotes (1983a) reported differences in yield loss among potato cultivars in untreated compared to nematicide-treated plots within a nematode-infested field. Tolerant cultivars had comparatively little yield decrease compared to intolerant cultivars. Their data also indicated that some nematode-resistant potato cultivars are intolerant to nematode attack. Results obtained in fields with a range of nematode population densities indicated that slopes of regression lines for yield of intolerant cultivars against initial nematode density are more negative than slopes for tolerant cultivars. The authors suggested that regressions of yield against initial nematode densities are better measures of tolerance than tolerance indices established by comparisons between nematicide-treated and untreated plots. Similarly, Dale et al. (1988) concluded that the selection of potato clones in a breeding program based on yield in *G. rostochiensis*-infested soil enhances selection for tolerance while also selecting for increased yield potential. Results of field and greenhouse experiments by Trudgill and Cotes (1983b) revealed reduced root length, root weight, and shoot:root weight ratios for nematode-intolerant compared to tolerant potato cultivars. Evans and Franco (1979) detected less dry matter accumulation of calcium (an indicator of drought tolerance in potato) in nematode-tolerant potato cultivars relative to intolerant cultivars, supporting suggestions that tolerance to nematode parasitism is related to tolerance to other agents of similar stresses. Interactions with other pathogens also have been proposed as a contributing factor of tolerance (Dale, 1988).

Tolerance of selected soybean cultivars and plant introductions (PIs) to *H. glycines* parasitism has been determined. Boerma and Hussey (1984) measured seed yield of 54 soybean cultivars and PIs in paired, nematicide-treated and nontreated field plots. A tolerance index (TI) was calculated for each cultivar and PI by dividing yield in untreated plots by yield in adjacent, treated plots, then multiplying by 100. A TI value of 100 indicated equal yield in both nematicide-treated and nontreated plots. The greater the yield reduction in the nontreated plots compared to the nematicide-treated plots, the lower the TI value. Boerma and Hussey detected tolerance in PI 97.100 (TI = 96), moderate tolerance in the cultivars 'Coker 156' and 'Wright' (TI = 68 to 95), and intolerance in 'Coker 237' and 'Bragg' (TI = 33 to 68). The experiments reported included determinate soybean cultivars adapted to the southern United States, whereas soybean cultivars grown in the Midwest are indeterminate in growth habit. Differences in length of flowering and reproductive periods between determinate and indeterminate cultivars may affect tolerance to *H. glycines*.

Use of nematicides for evaluation of tolerance in paired plot experiments may introduce artifacts that alter tolerance assessment. Nematicides may alter the form of soil nitrogen, affect plant growth, increase nematode activity at sub-lethal doses, and have undesirable non-target effects (Barker and Olthof, 1976; Barker et al., 1988). Therefore, alternative methods for tolerance determination have been proposed. Koenning et al. (1992) used multiple planting dates and periodic destruction of *H. glycines*-susceptible soybean plots within a single growing season as a method of generating a range of initial *H. glycines* population densities. Subsequently, they

evaluated yields of one *H. glycines*-resistant and two *H. glycines*-susceptible soybean cultivars within the field. Seed yield of intolerant 'Essex', but not that of moderately tolerant 'Coker 156', was negatively correlated with initial nematode population densities. The *H. glycines*-resistant cultivar 'Bedford' had greater seed yield than either *H. glycines*-susceptible cultivar. In similar field experiments with plots of varying initial *H. glycines* population densities, Alston and Schmitt (1987) reported seed yield of 'Coker 156' decreased quadratically with increasing initial nematode population densities at one location, but not at a second location where cooler temperatures and greater rainfall may have adversely affected the nematode.

Soybean growth in *H. glycines*-infested soil also has been determined under controlled conditions in greenhouse and growth chamber experiments. Miltner et al. (1991) compared shoot and root growth of 'Bragg' and 'Wright' soybeans in a rhizotron growth chamber at initial inoculum densities of 0, 100, and 1,000 *H. glycines* eggs per 100 cm^3 of soil. Root numbers of the moderately tolerant cultivar 'Wright' were stimulated by presence of the nematode, whereas vegetative and reproductive development of the plant were unaffected. In contrast, root numbers and plant development of the intolerant cultivar 'Bragg' were significantly reduced in the 1,000 eggs per 100 cm^3 of soil treatment. Abawi and Jacobsen (1984) reported negative correlations between initial nematode population densities and soybean growth in a greenhouse experiment. Plant dry weight of 'Amsoy 71' soybean in a six week greenhouse experiment decreased from 0.56 to 0.31 g as initial *H. glycines* densities increased from 0 to 4,800 eggs per 100 cm^3 soil. The results of Abawi and Jacobsen

were not compared to field experiments.

Several mechanisms of soybean tolerance to *H. glycines* parasitism have been suggested, but no specific mechanisms have been proven. Stimulation of root growth of moderately tolerant 'Wright' at low nematode population densities has been proposed as one possible tolerance mechanism (Miltner et al, 1991). Radcliffe et al. (1990) suggested that tolerance in 'Wright' is a result of the combined effects of compensatory root growth, deep-rooting patterns, and a more "efficient" plant. Evaluation of two drought-tolerant soybean lines did not reveal an association with *H. glycines* tolerance (Barker and Koenning, 1995). Width of syncytia produced in *H. glycines*-tolerant PI 97.100 was less than 50% of those produced in *H. glycines*-intolerant cultivar 'Essex' (Anand et al., 1993), indicating that syncytial size may be a component of tolerance in soybean. Other research results indicated that tolerance may be derived, in part, from formation of syncytia in cortical tissue versus the stele (Johnson et al., 1993). Most tolerance mechanism research has included only one nematode-tolerant cultivar, but evaluation of more than one *H. glycines*-tolerant cultivar likely is needed before the mechanisms involved can be determined.

Interaction of *H. glycines* with other soybean pathogens

Interactions between plant-parasitic nematodes and other plant pathogens, especially fungi, have been established and reviewed (Powell, 1971; Powell, 1979). However, relatively few research results investigating interactions between *H. glycines* and other pathogens have been reported (McGawley, 1992). In greenhouse and field microplot experiments, Ross (1965) illustrated that infection by *H. glycines* predisposed

'Lee' soybean to a greater severity of Fusarium wilt (*Fusarium oxysporum* Schlecht) than did infection by the root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood. The author suggested that differences between the two nematode species for mode of entry and intra-root migration contributed to the detected response differences. Ross also reported greater numbers of *H. glycines* females on *Fusarium*-infected 'Lee' than on *Fusarium*-free 'Lee'. Adeniji et al. (1975) reported that *Phytophthora sojae* Kaufmann & Gerdemann infection of 'Corsoy' and 'Dyer' soybean seedlings was more severe when associated with *H. glycines* infection than when the fungus was present alone. However, *P. sojae* resistance of 'Harosoy 63' was not affected by *H. glycines* infection, nor was *H. glycines* resistance in 'Dyer' affected by *P. sojae* infection, but *P. sojae* infection of 'Corsoy' reduced the number of *H. glycines* females produced.

Perhaps the most studied interaction between *H. glycines* and a fungal soybean pathogen is the interaction between *H. glycines* and *Fusarium solani* (Mart.) Sacc. f. sp. *glycines* form. nov. (Roy, 1997), the causal agent of soybean sudden death syndrome (SDS). Results of Hershman et al. (1990) and Rupe et al. (1991) indicate that SDS development in *H. glycines*-susceptible cultivars was greater than in *H. glycines*-resistant cultivars when soybean plants were grown in the presence of both pathogens. Additional research by McLean and Lawrence (1993) detected 40% fewer *H. glycines* eggs produced on plants exhibiting foliar symptoms of SDS than on soybeans without symptoms of the disease. Furthermore, they reported a negative correlation between foliar symptom ratings of SDS disease severity and total numbers of *H. glycines* cysts, eggs, and J2 produced. Plants of the *H. glycines*-susceptible cultivar 'Coker 156' had

greater incidence and severity of SDS in the presence of *H. glycines* compared to plants grown in the presence of the fungus alone.

Brown stem rot (BSR) of soybean, caused by the fungus *Phialophora gregata* (Allington & Chamberlain) Gams, is another important pathogen of soybean in the Midwest (Doupnik, 1993). The disease was first identified in Illinois in 1944 (Allington, 1946). External symptoms of BSR normally appear late in the growing season and include a dull brown discoloration of the stem and browning and necrosis of the leaves (Allington and Chamberlain, 1948). These external symptoms are not always apparent or may be confused with similar symptoms caused by other soybean pathogens. The most diagnostic symptom of BSR is a dark, reddish-brown discoloration of the vascular system and pith tissues of the plant extending from the soil line upward into the soybean stem. The fungus is widely distributed throughout the Midwest and can be detected in most fields every year (Tachibana and Booth, 1979), with greatest yield reductions occurring in years of cool, wet weather during podfill followed by hot, dry conditions late in the season (Sinclair, 1989). Estimates of soybean yield loss due to BSR range from 9 to 44 percent (Mengistu and Grau, 1987). *Phialophora gregata* has a limited host range (Allington and Chamberlain, 1948), and BSR management recommendations include rotation to nonhost crops and growing BSR-resistant cultivars (Sinclair, 1989; Tachibana and Card, 1979).

The wide distribution of *P. gregata* and *H. glycines* throughout the Midwest suggests that the potential of soybean being simultaneously infected by both pathogens is great. *Phialophora gregata* has been isolated from *H. glycines* cysts extracted from

field soil (Carris et al., 1986), and presence of *H. glycines* has been demonstrated to increase incidence of BSR of adzuki bean (*Vigna angularis*) in greenhouse experiments (Negishi and Kobayashi, 1984). Preliminary data (Behm and Tylka, unpub.; Tachibana, unpub.; Tubajika, Tylka, and Yang, unpub.) indicate the potential for the presence of *H. glycines* to increase the incidence and severity of BSR of soybean, although there are no published results of research investigating interactions between the two pathogens.

Summary

Growing *H. glycines*-susceptible soybean cultivars in infested fields is recommended to offset selection pressure exerted on the pathogen by repeated use of *H. glycines*-resistant cultivars. Use of *H. glycines*-tolerant, susceptible soybean cultivars may provide compensation for selection pressure while maintaining yield. Currently, no information about *H. glycines* tolerance of adapted soybean cultivars is available to Iowa growers. Additionally, development of a greenhouse or growth chamber assay for prediction of tolerance would expedite breeding efforts for *H. glycines*-tolerant cultivar development and provide growers with indicators of *H. glycines*-susceptible cultivar performance in infested fields.

Research examining interactions between *P. gregata* and *H. glycines* would provide valuable information for researchers and soybean growers, leading to better understanding of disease complexes between nematodes and fungi. A better understanding of the interaction of these two pathogens also would enhance effectiveness of field screening for *P. gregata* and *H. glycines* resistance in soybean breeding

programs and, ultimately, would provide information leading to more effective disease management strategies for Iowa soybean growers.

Dissertation Organization

This dissertation consists of an abstract, a general introduction with literature citations, two chapters presented as separate journal manuscripts, a general summary, and an appendix. The first paper, co-authored by G. L. Tylka and S. R. Cianzio, will be submitted to Crop Science, and the second paper, co-authored by G. L. Tylka, will be submitted to the Journal of Nematology for publication. Tables and figures follow the literature cited section within each paper. The appendix contains supplemental data from the first paper.

Abbreviations Used in Dissertation

The following are abbreviations used within the text of the dissertation: ANOVA, analysis of variance; BSR, brown stem rot; cfu, colony forming units; DAP, days after planting; Hgt, plant height; J2, second-stage juvenile; $Log_{10}(X)$, log_{10}-transformed nematode population data; LSD, least significant difference; PI, plant introduction; Pi, initial nematode population density; Pf, final nematode population density; PR2, nematode population density at R2; R1, beginning-bloom soybean growth stage; R2, full-bloom soybean growth stage; R7, soybean physiological maturity; R8,

soybean harvest maturity; Rdw, root dry weight; Rf, reproductive factor; RH, relative height; RW, relative seed weight; RY, relative yield; SCN, soybean cyst nematode; SDS, sudden death syndrome; Sdw, shoot dry weight; S:R, shoot:root weight ratio; TI, tolerance index; TOTALR, total reproductive period length.

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SOYBEAN TOLERANCE TO SOYBEAN CYST NEMATODE (*HETERODERA GLYCINES*, ICHINOHE)

A paper to be submitted to Crop Science

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Abbreviations: BSR, brown stem rot; DAP, days after planting; Hgt, plant height; $Log_{10}(X)$, log_{10}-transformed nematode population data; PI, plant introduction; Pi, initial nematode population density; Pf, final nematode population density; PR2, nematode population density at R2; R1, beginning-bloom soybean growth stage; R2, full-bloom soybean growth stage; R7, soybean physiological maturity; R8, soybean harvest maturity; Rdw, root dry weight; Rf, reproductive factor; RH, relative height; RW, relative seed weight; RY, relative yield; SCN, soybean cyst nematode; SDS, sudden death syndrome; Sdw, shoot dry weight; S:R, shoot:root weight ratio; TI, tolerance index; TOTALR, total reproductive period length.

ABSTRACT

Experiments were conducted in soybean cyst nematode (SCN)-infested and noninfested fields in 1994, 1995, and 1996 to evaluate SCN-susceptible soybean genotypes for tolerance to SCN. Inverse linear relationships of relative yield [RY=(individual plot yield÷experiment mean yield)×100] versus $\log_{10}$-transformed initial SCN soil egg population densities [Log_{10}(Pi+1)] were detected for all genotypes, including SCN-resistant 'Jack'. Magnitudes of linear regression slopes were indicators of tolerance. In the 1995 experiment, slope of RY versus Log_{10}(Pi+1) for SCN-susceptible 'CX366' (-6.16) did not differ from that for 'Jack' (-3.88); slopes for all other genotypes ranged from -7.40 for 'Probst' to -12.09 for 'Sturdy'. Tolerance indices [TI=(mean RY in infested fields÷mean RY in noninfested fields)×100]) ranged from 86.6 for 'Jack' to 67.6 for 'Sturdy' and were correlated (r=0.85) with regression slopes of RY versus Log_{10}(Pi+1). In 1996, slope of RY versus Log_{10}(Pi+1) for 'Jack' (-4.79) was less negative than slope for all susceptible genotypes in the experiment. 'Probst' had the least negative slope of RY versus Log_{10}(Pi+1) (-7.91) among the susceptible genotypes, and 'S19-90' had the most negative slope (-13.66). Slopes of RY versus Log_{10}(Pi+1) were correlated with TI (r=0.86) in 1996. Selected genotypes were grown in growth chamber pots containing soil infested with increasing SCN egg population densities. Inverse linear relationships between plant growth after eight weeks and initial egg inoculum densities were detected for all genotypes. However, regression slopes and TI of the genotypes in the growth chamber experiment were poorly correlated (r=-0.09 to 0.49) with ranking for regression slopes and TI from field

evaluations.

INTRODUCTION

Soybean cyst nematode, (*Heterodera glycines* Ichinohe; SCN), is estimated to be the most economically damaging pathogen of soybean (*Glycine max* (L.) Merrill) in the northcentral United States (Doupnik, 1993). The nematode is most effectively managed by rotation of nonhost crops and SCN-resistant soybean cultivars. Crop rotation practices that include growing a SCN-susceptible soybean cultivar periodically are recommended (Tylka, 1995) to offset selection pressure that occurs when SCN-resistant cultivars are grown repeatedly, thereby avoiding or delaying shifts in avirulence gene frequencies within a nematode population (Triantaphyllou, 1975; Young and Hartwig, 1988).

Resistance is a measure of the ability of a host plant to restrict nematode reproduction, whereas tolerance is the ability of a host plant to maintain growth and yield in the presence of nematode parasitism (Cook and Evans, 1987). Tolerant, SCN-susceptible soybean cultivars maintain acceptable yields without exerting selection pressure on nematode populations. In the past, tolerance indices of soybean cultivars to SCN parasitism have been calculated by comparing seed yield in paired, nematicide-treated and untreated plots in SCN-infested soils (Boerma and Hussey, 1984). However, nematicides may increase nematode activity at sub-lethal doses, alter forms of soil nitrogen, and adversely affect soybean growth (Barker and Olthof, 1976; Barker et al., 1988) and, therefore, influence tolerance evaluations. Additionally, nematicides

may not be effective in all soil types. Alternative methods of tolerance determination, such as regression analyses of soybean yield versus nematode soil population densities, have been proposed to avoid potential artifacts associated with nematicide use (Alston and Schmitt, 1987; Koenning et al., 1992). Trudgill and Cotes (1983) suggested that magnitude of slope for yield versus initial nematode population densities (Pi) can be used to differentiate among potato (*Solanum tuberosum* L.) genotypes for levels of potato cyst nematode (*Globodera rostochiensis* and *G. pallida*) tolerance.

To date, most research on plant tolerance to nematode parasitism has been done in the field. Development of a greenhouse assay for assessing tolerance would allow for evaluation of large numbers of lines which would be necessary for detecting tolerance in segregating populations and would expedite breeding efforts for SCN-tolerant cultivar development. Soybean growth response to a range of SCN population densities in greenhouse and growth chamber experiments has been reported as a means of assessing tolerance (Abawi and Jacobsen, 1984; Miltner et al., 1991), but no research relating SCN tolerance in field experiments to soybean growth in SCN-infested soil in greenhouse or growth chamber experiments has been published.

The objectives of this research were to evaluate selected, Iowa-adapted soybean genotypes for tolerance to SCN parasitism in naturally infested fields without nematicide application, and to develop greenhouse techniques for assessing SCN-tolerance by measuring soybean growth response to increasing nematode population densities and relating the results to those obtained in field evaluations.

MATERIALS AND METHODS

1994 field experiment

The 1994 field experiment was planted at four SCN-infested Iowa locations (Appendix Tables A-1 and A-2). Twenty-nine soybean genotypes were grouped into three maturity sets (north, central, and south) by adaptation for Iowa (Appendix Table A-3). Each maturity set contained one SCN-resistant and nine SCN-susceptible genotypes. The soybean genotypes were planted at a seeding rate of approximately 33 seeds m^{-1} of row in plots four rows wide and 4.6 m long; row spacing was 69 cm. Each maturity set was planted in each field as randomized complete blocks with four replications.

Initial, midseason (PR2), and final (Pf) SCN soil population densities were determined by arbitrarily collecting five 2.5-cm-diam., 20-cm-deep soil cores from the center 2.7 m of each of the two middle rows of each plot at planting and after the R2 and R7 (Fehr et al., 1971) soybean growth stages. Soil cores from each plot at each sampling date were combined and mixed, and SCN cysts were extracted from 100 cm^3 aliquants of soil by elutriation (Byrd et al., 1976) and collected on 250-μm-pore sieves. Soybean cyst nematode eggs were extracted from cysts and females with a motorized pestle, were recovered on a 25-μm-pore sieve, and were stained with acid fuchsin (Niblack et al., 1993) to facilitate counting by direct microscopic observation. Nematode egg data were used to calculate reproductive factors [Rf=(Pf÷Pi)] for each plot.

The number of days after planting to the R1 and R8 soybean reproductive stages

was determined for each plot at the Ames and Nevada locations. Days to R1 and R8 data were used to calculate total reproductive period length (TOTALR=R8-R1) for each genotype at the two locations. Chelated iron (Sequestrene, Ciba-Geigy, Greensboro, NC) was applied at 0.7 kg ha^{-1} on 6 and 16 June to alleviate symptoms of iron deficiency chlorosis at the Ames and Colo locations, respectively. Plant height of each plot at each location was measured prior to harvest. Each plot was end-trimmed to a final row length of 2.7 m prior to mechanical harvest of the middle two rows. Harvested seed was dried to 8% moisture, and seed yield (g $plot^{-1}$) was recorded for each plot. Yields were converted to kg ha^{-1} adjusted to 13.5% moisture. Seed weight (g 100^{-1} $seeds^{-1}$) also was determined for each plot. Soybean yield, plant height, and seed weight data were used to calculate relative yield [RY=(individual plot yield÷experiment mean yield)×100], relative height [RH=(individual plot height÷experiment mean height)×100], and relative seed weight [RW=(individual plot seed weight÷experiment mean seed weight)×100] for each plot.

Soybean and SCN data were subjected to analysis of variance (ANOVA), and Fisher's least significant difference (LSD) test (P=0.05) was used to separate means when significant differences among genotypes were detected (Cochran and Cox, 1992). Additionally, linear, quadratic, and cubic regressions of RY, RH, and RW versus $\log_{10}$-transformed SCN soil population densities [Log_{10}(Pi+1), Log_{10}(PR2+1), and Log_{10}(Pf+1)] were calculated for each soil sampling date.

SCN susceptibility test

A greenhouse experiment was conducted to compare the susceptibility of the SCN-susceptible genotypes to be used in the 1995 field experiment. One-wk-old seedlings of each genotype were transplanted into plastic conetainers containing approximately 100 cm^3 of a sterile, 3:1 sand-soil mix infested with approximately 5500 SCN race 3 eggs. The conetainers were arranged in a completely randomized design, with 12 replications per genotype, and were incubated at a constant temperature of 25°C. Twenty-seven days after transplanting, SCN females were dislodged from the roots of each plant by a stream of water, collected on a 250-μm-pore sieve, and counted by direct microscopic observation. Data were subjected to ANOVA, and a LSD test (P=0.05) was used to separate means when significant differences were detected among genotypes.

1995 field experiment

The 1995 field experiment was planted at three SCN-infested and two non-infested locations in Iowa (Table 1). One SCN-resistant and 19 SCN-susceptible soybean genotypes (Table 2) were planted in a randomized complete block design with eight replications at each location. Plot size and row spacing were identical to the 1994 field experiment, and data were collected and analyzed in the same manner as the 1994 experiment except that seven arbitrarily selected soil cores were collected from the center 2.7 m of each of the two middle rows of each plot at planting and after the R7 growth stage.

The number of days after planting to the R1 and R8 soybean growth stages was

determined for each plot at the Ames SCN-infested and noninfested locations. Seed yield (g $plot^{-1}$) and moisture (%) were determined for each plot at all locations, and the data were converted to kg ha^{-1} adjusted to 13.5% moisture. Seed yields were used to calculate tolerance indices [TI=(mean relative yield in SCN-infested fields÷mean relative yield in noninfested fields)×100] for each genotype.

BSR susceptibility test

To assess the potential for brown stem rot (BSR) to influence our SCN tolerance evaluations, the genotypes used in the 1995 field experiment were evaluated for susceptibility to BSR. Approximately 25 seeds of each genotype were planted in 1-m-long rows in the BSR evaluation nursery at the Iowa State University Curtiss Research Farm in Ames, Iowa, in two rows per genotype. After the R7 growth stage, the stems of ten arbitrarily selected plants from each row were measured for length, then the stems were split longitudinally and the length of stem discoloration characteristic of BSR infection from the soil line was determined. Brown stem rot severity was calculated for each plant by dividing the length of stem discoloration by the plant height and multiplying by 100. The severity data were averaged for each genotype, and the data were analyzed as described above.

1996 field experiment

The 1995 field experiment was repeated in 1996 at three SCN-infested and two non-infested locations in Iowa (Table 3). The experimental design and data collection and analysis were the same as the 1995 experiment with the following exceptions. The planted row length for the 1996 experiment was 3.7 m, and the middle two rows of

each plot were harvested without end-trimming. Soil cores were collected from the entire length of each of the middle two rows of each plot. Chelated iron was applied at the Napier location on 16 and 24 July using the same rate as for the 1994 experiment to alleviate symptoms of iron deficiency chlorosis. Days after planting to the R1 and R8 growth stages were recorded at the Ames SCN-infested and noninfested locations. Harvested seed from each plot was dried before weighing as in the 1994 experiment.

Greenhouse tolerance experiment

The soybean genotypes used in the 1995 and 1996 field experiments were evaluated for tolerance in a greenhouse experiment. Individual 1-wk-old seedlings of each genotype were transplanted into 1.75 L of a sterile, 1:1 sand-soil potting mix in 15-cm-diam. clay pots. The potting mix in each pot was infested with 0, 100, 500, 1000, 2000, or 4000 SCN race 3 eggs 100^{-1} cm^{-3}. A randomized complete block design with five replications was used. A temperature of 24°C ± 2 C° was maintained, and photoperiod was extended to 16 h per day with supplemental lighting. Two and four wks after transplanting 100 ml of 400 ppm N, water-soluble 20-10-20 (N:P:K) fertilizer was applied to each pot. Plant height (Hgt) from the cotyledonary node to the terminal node, and number of nodes per plant were measured at weekly intervals beginning one wk after transplanting. Eight wks after transplanting, the plants were severed at the cotyledonary node, and the plant roots were carefully rinsed free of adhering soil. Plant shoots and roots were oven dried at 100°C for 24 h, after which shoot (Sdw) and root dry weights (Rdw) were measured and a shoot:root dry weight ratio (S:R) was calculated for each plant. Final SCN egg population densities (100^{-1} cm^{-3} potting mix)

were determined for each pot using the procedures described in the above field experiments. Tolerance indices for Hgt and Sdw were calculated by genotype at each level of Pi by dividing Hgt or Sdw in the infested treatments by Hgt or Sdw in the noninfested treatments and multiplying by 100.

Soybean and SCN data were subjected to ANOVA, and a LSD test (P=0.05) was used to separate means when significant differences were detected among treatments. Additionally, linear regressions of Hgt and Sdw versus Pi were calculated.

Growth chamber tolerance experiment

Variability obtained in the greenhouse experiment indicated the need for a more controlled environment for evaluation of tolerance. Therefore, six soybean genotypes were selected, based on the results of the 1995 field experiment, for evaluation in a growth chamber experiment. One-wk-old seedlings of 'Jack' (SCN-resistant), 'CX366' (putative tolerant), 'Probst' (putative tolerant), 'S24-92' (putative moderately tolerant), 'BSR101' (putative intolerant), and 'Sturdy' (putative intolerant) were transplanted into 15-cm-diam. clay pots containing 1.75 L of sterile, 1:1 sand-soil mix infested with 0, 100, 500, 1000, 2000, or 4000 SCN race 3 eggs 100^{-1} cm^{-3}. The growth chamber experiment was conducted twice in a Conviron (Controlled Environments, Pembina, ND) model CMP3244 and once in a model CMP3023 growth chamber with three replications per genotype for each trial of the experiment. Temperature was maintained at 24°C $\pm$ 1 C° with a 16-h photoperiod. No fertilizer was applied in the growth chamber experiments. Data were collected and analyzed in the same manner as the greenhouse experiment described above.

RESULTS

1994 field experiment

Overall mean Pi ranged from 1736 eggs 100^{-1} cm^{-3} soil at the Ames location to 5569 eggs 100^{-1} cm^{-3} soil at Nevada (Appendix Table A-4). No differences in Pi among genotypes within a maturity set were detected at any location except the south maturity set at Nevada. Soybean cyst nematode soil egg population densities increased for all SCN-susceptible genotypes from the initial to the mid-season and final sampling dates and from the mid-season to final sampling dates (Appendix Tables A-4, A-5 and A-6). Nematode population densities decreased on all resistant cultivars, except 'Bell' at the Colo and Nevada locations. Overall mean Pf ranged from 5780 eggs 100^{-1} cm^{-3} at the Kanawha location to 22 469 eggs 100^{-1} cm^{-3} at Ames (data not shown). All SCN-susceptible genotypes had Rf greater than 1.0 at all locations, indicating SCN population densities increased during the growing season (Appendix Table A-7). Mean Rf across locations for 'Jack' and 'Yale' were less than 1.0, whereas 'Bell' had a mean Rf of 2.0.

Mean location yields ranged from 2486 kg ha^{-1} for the north maturity set at Kanawha to 3765 kg ha^{-1} for the south maturity set at Colo (Appendix Table A-8). The SCN-resistant cultivars in each maturity set had the greatest mean yield at each location, except for 'Yale' at Kanawha. Although linear regression models fit the distribution of the data better than quadratic or cubic models, few significant linear relationships were detected when a regression of RY versus $Log_{10}(Pi+1)$ was calculated (Appendix Table A-9). Additionally, five genotypes in the south maturity set had positive values for slope, indicating RY increased as Pi increased. Similar results were obtained with

regressions of RY versus $Log_{10}(PR2+1)$ and $Log_{10}(Pf+1)$ (Appendix Table A-10).

Few significant linear relationships were detected for regressions of RH or RW versus log_{10}-transformed egg data calculated for each sampling date (Appendix Tables A-11 through A-16). Results of linear regressions of days after planting to R1 and R8 and TOTALR versus log_{10}-transformed egg population densities for each sampling date are provided in Appendix Tables A-17 through A-25. Few significant linear relationships between the soybean reproductive data and log_{10}-transformed population densities were detected.

SCN susceptibility test

Results of the SCN susceptibility test revealed differences among genotypes for number of SCN females developed (Table 2). Mean number of females on 'Jack' was 7, whereas the SCN-susceptible genotypes had number of females ranging from 286 for 'CX298' to 486 for 'IA2007R'. The number of females on 'CX298' was less than that on A92-727017, 'IA2007R', 'IA2008R', and 'Kenwood 94', whereas the number of females on 'IA2007R' was greater than that of all other susceptible genotypes, except A92-727017, 'BSR101', 'IA2008R', and 'Kenwood 94'. No other differences in numbers of females among susceptible genotypes were detected.

1995 field experiment

Mean Pi in the SCN-infested fields were 2947, 3213, and 3683 eggs 100^{-1} cm^{-3} soil at the Kanawha, Ames, and Napier locations, respectively (Table 4). Significant differences in Pi among genotypes were detected at the Ames and Kanawha infested locations. Furthermore, several plots in each noninfested field had detectable SCN

population densities (Table 4). Mean Pf was greater than Pi for all genotypes, except 'Jack' (Tables 4 and 5). Location mean Pf of the SCN-infested fields ranged from 3584 eggs 100^{-1} cm^{-3} soil at Kanawha to 13 881 eggs 100^{-1} cm^{-3} soil at Napier. Experiment mean Rf for the SCN-susceptible genotypes ranged from 2.5 for 'S19-90' to 10.9 for 'CX329' (Table 6). All SCN-susceptible genotypes had an Rf value greater than 1.0 at all locations except 'S28-01' at the Kanawha infested location (0.8).

Mean location soybean yield ranged from 2393 kg ha^{-1} at the Kanawha infested location to 4148 kg ha^{-1} at the Ames noninfested location (Table 7). 'S24-92' had the greatest overall mean yield in the noninfested fields (4087 kg ha^{-1}), whereas SCN-resistant 'Jack' had the greatest overall mean yield (3351 kg ha^{-1}) in the SCN-infested fields. Mean yields in SCN-infested fields were less than those in noninfested fields for all genotypes, including 'Jack'.

Significant inverse linear relationships were detected between RY and $Log_{10}(Pi+1)$ for all genotypes, including 'Jack' (Table 8). Quadratic and cubic regression models did not fit the distribution of the data well. Regression slopes for RY versus $Log_{10}(Pi+1)$ ranged from -3.88 for 'Jack' to -12.09 for 'Sturdy'; slope for 'CX366' (-6.16) was not different from slope for 'Jack'. All other SCN-susceptible genotypes had slopes of RY versus $Log_{10}(Pi+1)$ significantly more negative than the slope for 'Jack'. 'S24-92' had the greatest value for mean RY (115.8) and regression Y intercept (135.2), whereas 'CX366' had the least mean RY (89.3) and Y intercept (101.1). There were no differences in $Log_{10}(Pi+1)$ among genotypes (Table 8). Tolerance indices ranged from 86.6 for 'Jack' to 67.6 for 'Sturdy' (Table 8) and were

correlated (r=0.85) to values for slope of RY versus $Log_{10}(Pi+1)$. Linear regression results of RY versus $Log_{10}(Pi+1)$ for 'Jack', 'CX366', 'S24-92', and 'Sturdy' are illustrated in Fig. 1.

Slopes for linear regressions of RH versus $Log_{10}(Pi+1)$ were significantly different from zero for all genotypes, except 'Jack' and 'IA2007R' (Table 9). 'Jack' had the greatest values for mean RH, regression slope, and Y intercept (119.7, -0.87, and 121.7, respectively). 'BSR101' had the most negative value for slope (-5.55), and 'S24-92' had the least mean RH (88.1) and regression Y intercept (95.6). Values for linear regression slopes of RW versus $Log_{10}(Pi+1)$ were significantly different from zero for all genotypes, except 'Jack' and 'AP3035' (Table 10). The slopes of RW versus $Log_{10}(Pi+1)$ for the remainder of the genotypes ranged from -1.96 for A92-727017 to -4.54 for 'BSR101'. Linear regression slopes of RY versus $Log_{10}(Pi+1)$ were correlated (r=0.70) with slopes for linear regressions of RH versus $Log_{10}(Pi+1)$, but only poorly correlated (r=0.44) with slopes of RW versus $Log_{10}(Pi+1)$. Linear regression analysis results of RY, RH, and RW versus $Log_{10}(Pf+1)$ are provided in Tables 11, 12, and 13, respectively. 'BSR101' had the most negative value for slope among the genotypes for linear regressions of RY, RH, and RW versus $Log_{10}(Pf+1)$. 'Jack', 'IA2007R', and 'AP3035' had the least negative value for linear regression slopes of RY, RH, RW versus $Log_{10}(Pf+1)$, respectively.

Results of the BSR susceptibility test revealed differences among genotypes for BSR severity (Table 2). Mean values for BSR severity ranged from 6.1% to 49.4%. Severity ratings of 'IA2008R' and 'BSR101' were less than that for all other genotypes

included in the test; 'IA2007R', 'Sturdy', 'AP3035', 'CX329', and A92-727017 had the greatest BSR severity.

1996 field experiment

Mean Pi in the SCN-infested fields were 1346, 1632, and 5078 eggs 100^{-1} cm^{-3} soil at the Napier, Kanawha infested, and Ames infested locations, respectively (Table 14), and no significant differences in Pi among genotypes were detected at any location. Several plots in each noninfested field had detectable SCN population densities (Table 14). Mean Pf values were less than Pi at the Ames SCN-infested, but greater than Pi at the Kanawha SCN-infested and Napier locations (Tables 14 and 15). Mean Rf for the SCN-susceptible genotypes ranged from 1.1 for A92-727017 and 'IA2008R' to 4.5 for 'CX366' (Table 16); Rf for 'Jack' was less than 1.0 at all locations.

Overall mean soybean yields ranged from 2784 kg ha^{-1} at Napier to 4618 kg ha^{-1} at the Ames noninfested location (Table 17). 'S24-92' had the greatest mean yield (4785 kg ha^{-1}) of all genotypes in noninfested fields, whereas 'Jack' had the greatest mean yield in SCN-infested fields (3667 kg ha^{-1}). Mean yield was less in SCN-infested compared to noninfested fields for all genotypes, including 'Jack'. Significant inverse linear relationships between RY and $Log_{10}(Pi+1)$ were detected for all genotypes, including SCN-resistant 'Jack' (Table 18). Quadratic and cubic regression models did not fit the distribution of the data well. Values for slope of RY versus $Log_{10}(Pi+1)$ ranged from -4.79 for 'Jack' to -13.66 for 'S19-90'. 'Jack' had the greatest mean RY (110.8) and 'S24-92' had the greatest value for regression Y intercept, whereas 'CX366' had the least mean RY (87.0) and Y intercept (105.1). Tolerance indices

ranged from 83.9 for 'Jack' to 62.7 for 'S19-90' and were correlated (r=0.86) with slopes of linear regressions of RY versus $Log_{10}(Pi+1)$. Results of linear regression analyses of RY versus $Log_{10}(Pi+1)$ for 'Jack', 'Probst', 'S24-92', and 'S19-90' are illustrated in Fig. 2.

Significant inverse linear relationships were detected between RH and $Log_{10}(Pi+1)$ for all genotypes, including 'Jack' (Table 19). Linear regression slopes of RH versus $Log_{10}(Pi+1)$ ranged from -4.39 for 'Jack' to -8.90 for 'BSR101'. 'Jack' had the greatest mean RH and regression Y intercept (121.6 and 131.0, respectively), whereas 'S19-90' had the least mean RH (86.4) and 'P9272' had the least Y intercept (100.4). Significant inverse linear relationships were detected for all genotypes when RW was regressed against $Log_{10}(Pi+1)$ (Table 20). Values for linear regression slopes of RW versus $Log_{10}(Pi+1)$ ranged from -1.96 for 'Jack' to -4.89 for 'Sturdy'. 'S19-90' had the greatest mean RW (130.5) and regression Y intercept (138.0). 'P9381' had the least mean RW value (88.2) and regression Y intercept (96.2); 'Jack' also had a regression Y intercept of 96.2. Linear regression slopes of RH and RW versus $Log_{10}(Pi+1)$ were poorly correlated (r=0.57 and 0.36, respectively) with slopes of linear regressions of RY versus $Log_{10}(Pi+1)$.

Linear regressions of RY, RH, and RW versus $Log_{10}(Pf+1)$ are presented in Tables 21, 22, and 23, respectively. 'Jack' had the least negative slopes for the linear regressions of RY, RH, and RW versus $Log_{10}(Pf+1)$. The most negative values for slope were detected for 'S19-90' (RY), 'BSR101' (RH), and 'Sturdy' (RW) versus $Log_{10}(Pf+1)$.

Combined 1995 and 1996 field experiment data

Soybean yield and Pi data from the 1995 and 1996 field experiments were combined for regression analysis of RY versus $Log_{10}(Pi+1)$ and TI (Table 24). Regression slopes for RY versus $Log_{10}(Pi+1)$ ranged from -4.92 for 'Jack' to -13.83 for 'Sturdy'. Slope for 'Jack' was significantly less than that for all SCN-susceptible genotypes in the experiment. 'S24-92' had the greatest value for mean RY (118.8) and regression Y intercept (145.5). 'CX366' had the least value for RY (93.4) and regression Y intercept (110.1). Tolerance indices ranged from 85.3 for 'Jack' to 65.0 for 'Sturdy' and were correlated ($r=0.86$) with values for slope of RY versus $Log_{10}(Pi+1)$. Based on the results of the combined 1995 and 1996 data 'CX298', 'CX366', and 'Probst' were the most tolerant and 'P9272' and 'Sturdy' were the most intolerant genotypes that we evaluated. The remainder of the genotypes were categorized as moderately tolerant.

It was not possible to conduct ANOVA analyses on the days after planting to R1 and R8 and TOTALR data within individual years because of the lack of independent replications, so data from the 1995 and 1996 field experiments were combined for analysis (Table 25). Differences in days after planting to R1 and R8 and TOTALR between SCN-infested and noninfested fields were detected for 11, eight, and seven genotypes, respectively. No significant correlations between days to R1 or R8 or TOTALR data and linear regression slopes of RY versus $Log_{10}(Pi+1)$ were detected for any of the genotypes.

Greenhouse tolerance experiment

Results of the greenhouse experiment revealed no differences in numbers of nodes per plant among Pi levels for any genotype (Table 26). Plant height, Sdw, Rdw, and S:R decreased as Pi increased for all genotypes, although few significant differences among inoculum levels were detected. Nematode soil population densities increased at each level of Pi for each genotype, except 'Jack'. Linear regressions of Hgt and Sdw versus Pi were significant for two and 13 genotypes, respectively (Table 27). Similarly, few significant differences were detected among genotypes or among Pi within genotypes for TI calculated for Hgt and Sdw (Tables 28 and 29, respectively).

Growth chamber experiment

Generally, all plant growth parameter values decreased as Pi increased for all genotypes, except Rdw of 'Jack' (Table 30). Final SCN soil population densities for 'Jack' increased with increasing Pi, whereas no consistent trend for Pf was detected among the SCN-susceptible genotypes. Reproductive factors for all genotypes decreased as Pi increased.

Significant inverse relationships were detected for linear regressions of Hgt and Sdw versus Pi for all genotypes, including 'Jack' (Table 31). Values for linear regression slopes of Hgt (-0.0150) and Sdw (-0.00034) versus Pi for 'Jack' were less negative than values for slopes of the SCN-susceptible genotypes. 'BSR101' had the least negative linear regression slope among the SCN-susceptible genotypes for Hgt (-0.0265) and Sdw (-0.00052) versus Pi, whereas 'CX366' had the most negative slope of Hgt (-0.0654) and Sdw (-0.00062) versus Pi. Differences among genotypes for

linear regression slope of Sdw versus Pi were not significant at $P=0.05$.

Tolerance indices for Hgt and Sdw of each genotype decreased as Pi increased (Table 32). 'Jack' had the greatest TI of all genotypes for Hgt and Sdw at each Pi level, whereas 'Sturdy' had the greatest mean TI for Hgt (65) and Sdw (24) among the SCN-susceptible genotypes. 'CX366' had the least TI for Hgt (48), and 'BSR101' had the least TI value for Sdw (17).

DISCUSSION

Different levels of tolerance to SCN parasitism were detected among the SCN-susceptible soybean genotypes studied in our field experiments based on yields of the genotypes in SCN-infested and noninfested plots. Tolerant cultivars had less negative values for regression slopes of RY versus $Log_{10}(Pi+1)$ and greater tolerance indices than intolerant cultivars. Additionally, Y intercepts of such regressions were indicators of yield potential in the absence of nematodes.

Genotype ratings for BSR susceptibility did not correlate well with tolerance ratings in our 1995 and 1996 field experiments (r=-0.11 and -0.35, respectively). Similarly, results of the SCN susceptibility test did not consistently correlate with field tolerance ratings in 1995 and 1996 (r=-0.73 and -0.50, respectively) or with Rf values in 1995 and 1996 (r=0.42 and 0.19, respectively). Consequently, it is unlikely that differences in genotype susceptibility to BSR or in magnitude of SCN reproduction affected our evaluation of the soybean genotypes for SCN tolerance. Although no significant differences in susceptibility to SCN were detected between the most tolerant

and least tolerant genotypes in our experiments, all genotypes should be evaluated for susceptibility to SCN prior to tolerance evaluation to distinguish resistant from susceptible genotypes.

Natural variation in SCN Pi within and among our experimental locations was sufficient for tolerance determination using linear regressions of RY versus $Log_{10}(Pi+1)$ when eight replications per location were planted. Unfortunately, we were unable to include a known tolerant, SCN-susceptible genotype as a control in our field experiments because previously described tolerant genotypes are not adapted to Iowa. Therefore, we included SCN-resistant 'Jack' as a control treatment in the experiments.

Results of the 1994 field experiment were inconclusive for evaluating tolerance of the genotypes, but revealed the necessity of including noninfested locations in the experimental design. Relative yields were calculated to compensate for differences in yield potential among the experiment locations, and log_{10} transformation was used to normalize the nematode population data. Linear regression models of RY versus $Log_{10}(Pi+1)$ provided the best fit to our data when compared to quadratic and cubic regressions or regressions with non-transformed Pi data. However, relatively few plots had Pi values in the 0 to 1000 range, and a more uniform distribution of Pi values may have resulted in a better fit to the non-linear models.

We observed inverse linear relationships between RY and $Log_{10}(Pi+1)$ for all genotypes, including SCN-resistant 'Jack', in 1995 and 1996. These results suggest that yield loss occurs with SCN-resistant cultivars at high nematode population densities and support the findings of Francl and Dropkin (1986), MacGuidwin et al. (1995), and

Tylka and Souhrada (1997). Among the SCN-susceptible genotypes, 'CX366', 'Probst', and 'CX298' had the least negative values for linear regression slope of RY versus $Log_{10}(Pi+1)$ when data from 1995 and 1996 were combined; these cultivars were classified as tolerant. Conversely, the genotypes with the most negative values for linear regression slope of RY versus $Log_{10}(Pi+1)$, 'P9272' and 'Sturdy', were categorized as intolerant. Genotypes with slopes of RY versus $Log_{10}(Pi+1)$ intermediate to the tolerant and intolerant genotypes were categorized as moderately tolerant. Variability of values for linear regression slope of RY versus $Log_{10}(Pi+1)$ between years among the moderately tolerant genotypes was greater than that observed among the tolerant or intolerant genotypes, although overall, slopes in 1995 and 1996 were relatively well-correlated ($r=0.72$).

Interestingly, we found that tolerance to SCN is either completely independent of or inversely related to overall yield potential of the soybean genotypes that we evaluated. The least tolerant genotypes ('Sturdy' in 1995 and 'S19-90' in 1996) had RY greater than the most tolerant genotypes across all Pi levels in 1995 and at Pi less than 1000 eggs 100^{-1} cm^{-3} soil in 1996. Similarly, the moderately tolerant 'S24-92' had greater RY than tolerant genotypes at all levels of Pi in both years and greater RY than the resistant genotype at low to moderate Pi values. The RY of the SCN-susceptible genotypes with the least negative linear regression slope of RY versus $Log_{10}(Pi+1)$ in both years ('CX366' in 1995 and 'Probst' in 1996) was less than 'Jack' across all Pi levels. Mean values for linear regression slope of RY versus $Log_{10}(Pi+1)$ were more negative in 1996 than in 1995, indicating greater yield reductions attributable to SCN

occurred in 1996. The greater yield reduction may have resulted in lowered carrying capacity of the plants explaining the lower Rf values in 1996 than in 1995.

The magnitude of slopes for linear regressions of RY versus $Log_{10}(Pi+1)$ were not strongly correlated to that of RH or RW versus $Log_{10}(Pi+1)$ ($r=0.36$ to 0.70, respectively) within or among years, indicating that yield loss caused by SCN parasitism is not solely attributable to reduced plant height or seed weight. Our data also revealed that values for Pf and Rf were poorly correlated ($r=-0.21$ to 0.47) to values for linear regression slope of RY versus $Log_{10}(Pi+1)$ in 1995 and 1996 and do not support previous research detecting greater reproduction on tolerant than on intolerant soybean cultivars (Koenning et al., 1992). However, tolerance of the genotypes evaluated in our experiments and that of genotypes evaluated in other experiments may be derived from different mechanisms having distinct effects on SCN reproduction. Also, the linear regression slopes of RY versus $Log_{10}(Pi+1)$ were correlated well with linear regression slopes for RY versus $Log_{10}(Pf+1)$ in 1995 and 1996 ($r=0.82$ and 0.91, respectively), although Pi commonly is used as a predictor of potential yield loss attributable to nematode parasitism. Leaf symptoms typical of SCN infection were not observed in 1995, and although several plots in the 1994 Nevada and 1996 Ames infested locations expressed leaf symptoms of SCN-infection, no association between tolerance and leaf symptom expression was detectable.

The inclusion of noninfested locations in the field experiment facilitated calculation of TI based on relative genotype yield in SCN-infested versus noninfested fields. Tolerance indices correlated well with values for linear regression slopes of RY

versus $Log_{10}(Pi+1)$ in 1995 and 1996 ($r= 0.85$ and 0.86, respectively) and could be used effectively for predicting tolerance as indicated by regressions of RY versus $Log_{10}(Pi+1)$. Tolerance evaluation based on yield comparisons between SCN-infested and noninfested fields is less labor intensive than evaluation based on determining Pi for each plot in an experiment and, in fact, may be a better indicator of tolerance because the lack of Pi values in the 0 to 100 range may have affected how well the various regression models fit the data. Our results support the hypothesis of Dale et al. (1988) that selection of genotypes for yield in nematode-infested fields coupled with yield data obtained in noninfested fields will facilitate selection of high-yielding, nematode-tolerant cultivars.

Results of greenhouse and growth chamber tolerance evaluations did not correlate well with field experiment results. In the greenhouse experiment, few significant relationships were detected for slopes of linear regressions of Hgt and Sdw versus Pi, and no differences for TI were detected among the genotypes at any level of Pi. Significant inverse linear relationships between plant growth and Pi were revealed by analysis of the growth chamber data. However, the values for slope of plant growth versus Pi were poorly correlated ($r=-0.09$ to 0.49) with results of the field experiments, except that 'Jack' had the least negative linear regression slope of height and weight versus Pi in the growth chamber and the least negative linear regression slope of RY versus $Log_{10}(Pi+1)$ in the field experiments. The tolerant 'CX366' (based on results of the field experiments) had the most negative slope in the growth chamber experiment, whereas the intolerant 'BSR101' (based on results of the 1995 field experiment) had the

least negative slope among the SCN-susceptible genotypes evaluated. Similar discrepancies between field and growth chamber experiments were detected for TI data.

In summary, we have determined that soybean genotypes can be evaluated for SCN tolerance in field experiments without the use of nematicides by utilizing natural nematode Pi variability within and among fields. In our studies, the magnitude of linear regression slopes of RY versus $Log_{10}(Pi+1)$ were indicators of tolerance differences among genotypes, and linear regression Y intercepts were indicators of yield potential of the genotypes in the absence of the nematode. Tolerance indices calculated from comparison of RY in SCN-infested soils versus RY in noninfested soils correlated well with linear regression slopes of RY versus $Log_{10}(Pi+1)$, and TI determinations are a less labor intensive method of determining tolerance. The lack of a consistent correlation between the linear regression slopes of RY versus $Log_{10}(Pi+1)$ and TI in 1995 and 1996 suggest the necessity of multiple year evaluations to accurately determine SCN tolerance. Results of greenhouse and growth chamber experiments were poorly correlated to field experiments, and, therefore, screening of early generation material in a soybean breeding program for SCN tolerance may not be feasible. However, field evaluations can be used to evaluate existing cultivars for tolerance, and the information used for selecting high-yielding, SCN-susceptible cultivars for use in crop rotation programs.

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Table 1. Planting, harvest, and soil sampling dates and soil characteristics for the 1995 field experiment.

				Sample dates		Texture (%)					
Location	Race	Plant	Harvest	Initial	Final	Clay	Sand	Silt	Soil class	O.M.†	pH
Ames (N)‡	NA§	24 May	10 October	25 May	12 October	24.2	41.4	34.4	Loam	4.7	7.2
Kanawha (N)	6	12 May	12 October	12 & 17 May	16 October	38.2	23.4	38.4	Clay Loam	6.4	6.8
Ames (I)	9	22 May	10 October	24 & 25 May	10 October	26.2	41.1	32.4	Clay Loam	4.3	6.8
Kanawha (I)	1	12 May	12 October	16 May	13 October	32.6	33.4	34.0	Clay Loam	5.3	6.7
Napier (I)	1	26 May	11 October	26 May	11 October	30.2	33.4	36.4	Clay Loam	7.0	7.7

† Percent organic matter.

‡ N = noninfested location; I = SCN-infested location.

§ NA = not available because insufficient numbers of SCN eggs were recovered for race determination.

Table 2. Phytophthora root rot (PRR) resistance genes, disease ratings, and susceptibility to SCN of soybean genotypes evaluated in 1995 and 1996 field experiments.

Genotype	PRR resistance†	PRR rating‡	BSR§	Females per plant¶
A92-727017	S	4.0	41.8	399
Agripro AP3035	S	1.9	43.0	340
BSR101	Rps1a	3.2	12.2	384
DeKalb CX298	Rps1k	-	30.4	286
DeKalb CX329	Rps1k	-	42.0	317
DeKalb CX366	Rps1c	-	34.5	289
IA2007R	Rps1k	1.7	49.4	486
IA2008R	Rps1k	1.9	6.1	397
IA2022	S	-	37.1	293
Jack	S	3.6	27.2	7
Kenwood 94	Rps1k	1.9	31.0	435
Northrup King S19-90	Rps1c	3.7	37.5	340
Northrup King S24-92	S	3.2	37.3	311
Northrup King S28-01	Rps1c	3.9	37.9	365
Pioneer P9272	S	3.2	34.8	308
Pioneer P9273	S	3.7	28.9	316
Pioneer P9303	S	3.6	27.0	366
Pioneer P9381	S	3.2	34.8	350
Probst	Rps1k	1.4	18.1	365
Sturdy	Rps1a	3.1	43.5	341
LSD(0.05)			11.6	107

† Genes for resistance to Phytophthora root rot; S = susceptible.

‡ Greenhouse evaluation of field tolerance to Phytophthora root rot taken from Iowa soybean yield test reports (Iowa State University Extension. AG 18-5. Ames) from 1991 to 1994. Ratings are on a scale of 1 = no dead plants or stunting to 5 = all plants dead.

§ Values are average percent stem discoloration at R7 growth stage at Iowa State University Curtiss Farm BSR evaluation nursery, 1995.

¶ Mean number of SCN females per plant in 28 day susceptibility assay with 12 replications per genotype.

Table 3. Planting, harvest, and soil sampling dates and soil characteristics for the 1996 field experiment.

				Sample date		Texture (%)				
Location	Race	Plant	Harvest	Initial	Final	Clay	Sand	Silt	Soil class	pH
Ames (N)†	NA‡	18 May	12 October	21 May	14 October	25.8	45.8	28.4	Loam	6.9
Kanawha (N)	NA	6 May	11 October	7 May	15 October	35.0	27.0	38.0	Clay loam	6.9
Ames (I)	1	21 May	12 October	21 May	4 October	21.8	45.8	32.4	Loam	7.2
Kanawha (I)	6	6 May	11 October	7 May	3 October	32.6	35.8	31.6	Clay loam	6.6
Napier (I)	3	18 May	14 October	21 May	4 October	27.0	39.0	34.0	Clay loam	7.7

† N = Noninfested location; I = SCN-infested location.

‡ NA = not available because insufficient numbers of SCN eggs were recovered for race determination.

Table 4. Initial SCN population densities for the 1995 field experiment, by genotype and location.

	Noninfested†			Infested			
Genotype	Ames	Kanawha	Mean	Ames	Kanawha	Napier	Mean
A92-727017	0	206	103	3875	5106	2554	3845
AP3035	38	31	35	2353	3475	3733	3187
BSR101	13	650	332	2475	3738	1765	2659
CX298	6	63	35	3618	1956	4879	3484
CX329	13	13	13	1860	4181	4024	3355
CX366	31	0	16	4103	1344	4207	3218
IA2007R	25	131	78	2132	3613	2606	2784
IA2008R	44	13	29	2632	3344	2912	2963
IA2022	6	25	16	2489	2150	3207	2615
Jack	13	169	91	2932	2988	2862	2927
Kenwood 94	63	6	35	2889	3164	2894	2982
P9272	31	569	300	4050	1988	2707	2915
P9273	56	319	188	2706	2100	5134	3313
P9303	19	19	19	2760	2594	4179	3178
P9381	81	256	169	3475	2988	4881	3781
Probst	25	81	53	3389	2663	2854	2969
S19-90	25	6	16	3232	2850	4980	3687
S24-92	13	244	129	3914	2356	2899	3056
S28-01	63	400	232	3264	2869	2060	2731
Sturdy	6	13	10	2775	3475	2771	3007
Mean	29	161	95	2947	3213	3683	3133
LSD(0.05)	NS‡	NS	NS	1482	2273	NS	NS

Values presented are eggs 100^{-1} cm^{-3} soil and are means of eight replications per location.

† Noninfested locations had several plots with detectable SCN population densities.

‡ NS = not significant.

Table 5. Final SCN population densities for the 1995 field experiment, by genotype and location.

	Noninfested†			Infested			
Genotype	Ames	Kanawha	Mean	Ames	Kanawha	Napier	Mean
A92-727017	0	1350	675	14 738	4163	16 214	11 675
AP3035	25	1263	644	13 069	3138	16 206	10 804
BSR101	25	1600	813	8 141	5363	11 398	8 301
CX298	13	2281	1147	10 098	3538	17 137	10 258
CX329	125	388	257	17 341	4463	10 689	10 831
CX366	25	663	344	15 912	3350	13 656	10 973
IA2007R	38	1713	876	15 698	4213	17 029	12 313
IA2008R	50	1175	613	10 426	3025	17 102	10 184
IA2022	0	563	282	9 469	4288	15 699	9 819
Jack	0	325	163	1 233	881	2 122	1 412
Kenwood 94	50	1563	807	11 883	3475	10 674	8 677
P9272	0	2438	1219	9 600	3850	14 718	9 389
P9273	13	2200	1107	8 662	5150	14 640	9 484
P9303	0	638	319	7 955	4344	16 167	9 489
P9381	25	1475	750	12 069	3063	8 857	7 996
Probst	13	613	313	15 155	3613	17 904	12 224
S19-90	13	138	76	4 612	3613	10 075	6 100
S24-92	0	1938	969	7 045	2763	12 650	7 486
S28-01	38	3738	1888	7 862	1519	18 319	9 233
Sturdy	25	767	396	13 863	3869	16 371	11 368
Mean	24	1341	683	10 742	3584	13 881	9 402
LSD(0.05)	NS‡	NS	NS	5305	NS	NS	5011

Values presented are eggs 100^{-1} cm^{-3} soil and are means of eight replications per location.
† Noninfested locations had several plots with detectable SCN population densities.
‡ NS = not significant.

Table 6. Reproductive factors† for soybean genotypes included in the 1995 field experiment, by genotype and location.

	Noninfested‡			Infested			
Genotype	Ames	Kanawha	Mean	Ames	Kanawha	Napier	Mean
A92-727017	0.1	5.2	2.7	7.0	1.4	19.0	6.5
AP3035	0.2	16.3	8.3	11.3	1.6	4.6	6.0
BSR101	0.3	2.5	1.4	7.0	2.1	6.1	4.8
CX298	0.3	43.7	22.0	3.7	3.1	2.8	3.3
CX329	6.9	1.6	4.3	22.1	4.0	3.1	10.9
CX366	0.3	0.0	0.2	7.0	5.6	4.9	5.9
IA2007R	1.0	13.6	7.3	12.3	3.3	25.6	9.6
IA2008R	0.2	3.3	1.8	4.9	3.3	6.9	5.0
IA2022	0.0	17.6	8.8	4.5	10.9	14.0	9.2
Jack	0.4	3.1	1.8	0.6	0.5	0.4	0.5
Kenwood 94	0.1	7.8	4.0	6.7	5.1	2.6	5.3
P9272	0.3	13.1	6.7	3.3	4.0	10.6	5.3
P9273	0.2	4.6	2.4	4.2	12.7	3.2	7.2
P9303	0.6	30.0	15.3	4.8	6.0	4.7	5.2
P9381	0.6	8.9	4.8	5.5	1.6	2.7	3.3
Probst	0.3	3.5	1.9	5.7	2.3	5.7	4.0
S19-90	0.3	7.4	3.9	2.2	2.8	2.5	2.5
S24-92	1.1	14.3	7.7	2.2	2.9	6.2	3.1
S28-01	0.5	8.5	4.5	4.0	0.8	6.5	3.1
Sturdy	0.4	4.3	2.4	7.2	2.4	16.8	8.4
Mean	0.7	10.5	5.6	6.3	3.8	7.4	5.8
LSD(0.05)	0.7	NS§	NS	5.1	NS	NS	6.2

Values presented are means of eight replications per location.

† Reproductive factor = final SCN egg population density÷initial SCN egg population density.

‡ Noninfested locations had several plots with detectable SCN population densities.

§ NS = not significant.

Table 7. Yield of soybean genotypes included in the 1995 field experiment by, genotype and location.

	Noninfested				Infested				
Genotype	Ames	Kanawha	Mean	Rank	Ames	Kanawha	Napier	Mean	Rank
A92-727017	4091	3014	3553	16	3000	2146	2636	2594	16
AP3035	4146	3477	3812	9	3299	2459	2512	2757	13
BSR101	4148	3669	3909	6	3361	2639	2403	2801	8
CX298	3683	2990	3337	19	2970	2096	2232	2433	19
CX329	3845	3047	3446	18	2738	1947	2411	2365	20
CX366	3710	2854	3282	20	2837	1995	2525	2452	18
IA2007R	4069	3213	3641	15	3009	2164	2195	2456	17
IA2008R	4118	3792	3955	5	3166	2577	2597	2780	11
IA2022	4154	3573	3864	7	3336	2627	2637	2867	4
Jack	4140	3297	3719	13	3789	2664	3600	3351	1
Kenwood 94	4246	3765	4006	2	3195	2678	2673	2849	5
P9272	4098	3430	3764	11	3236	2406	2656	2766	12
P9273	4162	3418	3790	10	3340	2525	2556	2807	7
P9303	4072	3332	3702	14	3304	2479	2616	2800	9
P9381	4196	2896	3546	17	3373	2190	2322	2628	15
Probst	4166	3332	3749	12	3146	2376	2821	2781	10
S19-90	4283	3386	3835	8	3499	2440	2563	2834	6
S24-92	4606	3567	4087	1	3644	2891	3085	3207	2
S28-01	4669	3325	3997	4	3327	2308	3085	2907	3
Sturdy	4361	3637	3999	3	3345	2250	2642	2746	14
Mean	4148	3351	3750		3246	2393	2638	2759	
LSD(0.05)	248	284	404		158	154	183	276	

Values presented are kg ha^{-1} and are means of eight replications per location.

Table 8. Tolerance indices† (TI) and results of linear regression analysis of relative yield‡ (RY) versus $\log_{10}$-transformed initial SCN population densities [(eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pi+1)$] for the 1995 field experiment. Genotypes are listed in decreasing value for slope.

	Mean						
Genotype	RY	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2	TI	TI rank
Jack	110.4	2.1	-3.88	118.6	0.12	86.6	1
CX366	89.3	1.9	-6.16	101.1	0.31	75.9	2
Probst	103.5	1.9	-7.40	117.6	0.35	74.7	5
CX298	91.3	1.9	-7.79	106.3	0.44	73.6	9
IA2022	105.4	1.9	-8.58	121.6	0.49	75.0	4
AP3035	105.4	1.9	-8.58	122.0	0.49	73.2	10
P9303	101.1	2.1	-8.62	119.4	0.47	73.7	8
A92-727017	96.4	2.0	-9.02	114.8	0.52	70.6	16
P9273	103.2	2.3	-9.05	124.3	0.39	72.1	12
S19-90	103.3	2.1	-9.17	122.6	0.48	72.6	11
P9381	99.2	2.4	-9.21	125.5	0.25	74.6	6
S24-92	115.8	2.0	-9.65	135.2	0.51	75.1	3
Kenwood 94	109.3	2.0	-10.07	129.3	0.66	72.1	12
CX329	91.2	1.9	-10.31	110.3	0.65	68.0	19
P9272	102.0	2.4	-10.52	126.9	0.50	71.8	14
IA2008R	104.4	2.2	-10.63	128.1	0.54	70.9	15
IA2007R	96.8	2.0	-11.08	119.5	0.55	68.8	17
S28-01	108.1	2.4	-11.11	134.6	0.30	74.4	7
BSR101	105.4	2.2	-11.64	131.2	0.67	68.8	17
Sturdy	103.7	2.1	-12.09	128.8	0.63	67.6	20
LSD(0.05)	9.6	NS§	2.29				

† TI = (mean relative yield in SCN-infested fields÷mean relative yield in noninfested fields)×100.
‡ RY = (individual plot yield÷experiment mean yield)×100.
§ NS = not significant.

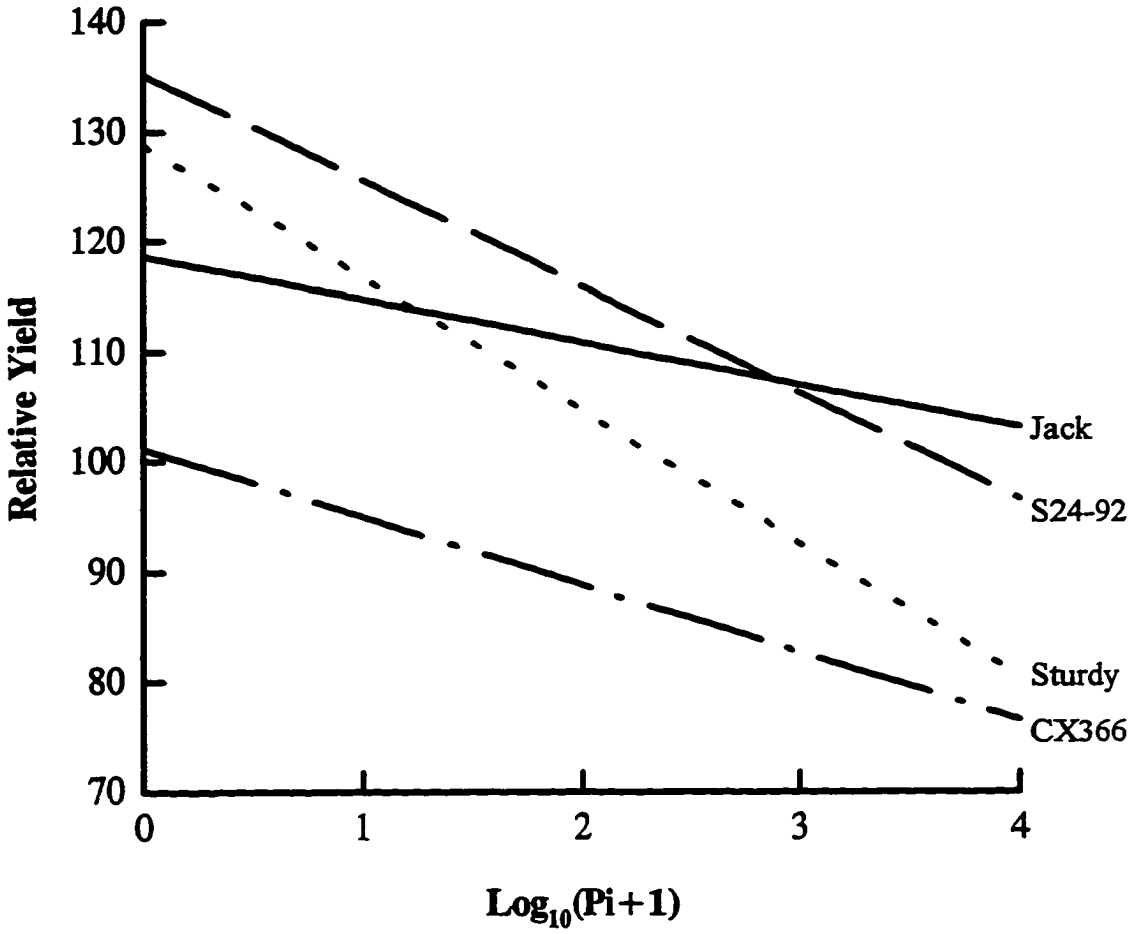

Fig. 1. Linear regression lines of relative yield [(individual plot yield÷experiment mean yield)×100] versus $\log_{10}$-transformed initial SCN egg population densities [Log_{10}(Pi+1)] for SCN-resistant 'Jack' (Y=118.6 - 3.88X), putative tolerant 'CX366' (Y=101.1 - 6.16X), putative moderately tolerant 'S24-92' (Y=135.2 - 9.65X), and putative intolerant 'Sturdy' (Y=128.8 - 12.09X) for the 1995 field experiment.

Table 9. Results of linear regression analysis of relative plant height† (RH) versus log_{10}-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pi+1)$] for the 1995 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RH	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2
Jack	119.7	2.1	-0.87 NS	121.7	0.03
IA2007R	98.3	2.0	-1.98 NS	102.5	0.07
CX366	116.9	1.9	-2.01 *	120.8	0.11
Kenwood 94	98.8	2.0	-2.79 *	104.6	0.18
IA2022	108.1	1.9	-2.80 *	113.5	0.14
P9303	95.4	2.1	-2.81 **	101.5	0.21
CX298	99.6	1.9	-3.24 **	106.0	0.37
AP3035	94.3	1.9	-3.24 **	100.7	0.27
Probst	104.6	1.9	-3.28 **	110.9	0.40
IA2008R	106.1	2.2	-3.31 *	113.5	0.15
CX329	103.0	1.9	-3.38 **	109.2	0.35
A92-727017	108.0	2.0	-3.40 **	114.9	0.37
S24-92	88.1	2.0	-3.68 **	95.6	0.26
P9381	101.1	2.4	-3.68 *	110.2	0.17
P9273	88.6	2.3	-3.83 **	97.5	0.25
Sturdy	96.7	2.1	-4.38 **	105.8	0.23
P9272	94.9	2.4	-4.49 **	105.4	0.38
S19-90	89.6	2.1	-4.57 **	99.3	0.32
S28-01	89.5	2.4	-5.05 **	101.7	0.27
BSR101	96.6	2.2	-5.55 **	109.1	0.40
LSD(0.05)	4.9	NS‡	1.36		

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† RH = (individual plot height÷experiment mean height)×100.

‡ NS = not significant.

Table 10. Results of linear regression analysis of relative seed weight† (RW) versus log_{10}-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pi+1)$] for the 1995 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RW	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2
Jack	90.0	2.1	-1.01 NS	92.0	0.05
AP3035	99.1	1.9	-1.11 NS	101.2	0.08
A92-727017	91.0	2.0	-1.96 **	95.0	0.21
CX366	96.3	1.9	-2.02 *	100.1	0.13
P9303	107.4	2.1	-2.07 *	111.8	0.16
IA2007R	105.9	2.0	-2.13 *	110.2	0.18
S24-92	101.0	2.0	-2.19 **	105.3	0.30
P9272	101.0	2.4	-2.23 **	106.3	0.19
IA2022	97.9	1.9	-2.27 **	102.1	0.26
P9273	95.1	2.3	-2.35 **	100.5	0.17
S28-01	92.7	2.4	-2.44 **	98.4	0.22
P9381	90.8	2.4	-2.56 *	96.9	0.18
Sturdy	113.1	2.1	-2.69 **	118.7	0.18
Kenwood 94	97.1	2.0	-2.95 **	103.1	0.50
Probst	95.7	1.9	-2.96 **	101.3	0.31
CX329	90.4	1.9	-3.06 **	96.7	0.52
IA2008R	97.7	2.2	-3.27 **	105.0	0.40
S19-90	120.9	2.1	-3.52 **	128.3	0.37
CX298	99.2	1.9	-4.07 **	106.9	0.35
BSR101	110.3	2.2	-4.54 **	120.3	0.43
LSD(0.05)	15.3	NS‡	1.18		

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Seed weight = g 100^{-1} $seeds^{-1}$; RW = (individual plot seed weight÷experiment mean seed weight)×100.

‡ NS = not significant.

Table 11. Results of linear regression analysis of relative yield† (RY) versus log_{10}-transformed final SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1995 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RY	$Log_{10}(Pf+1)$	Slope	Y intercept	R^2
Jack	107.8	1.7	-5.35	117.2	0.17
CX366	87.4	2.5	-6.36	103.4	0.35
AP3035	102.6	2.4	-6.76	118.5	0.35
CX298	88.2	2.6	-7.39	107.4	0.40
IA2022	103.1	2.2	-7.46	119.4	0.50
P9303	98.4	2.5	-7.46	116.7	0.48
P9381	96.6	2.3	-8.03	115.6	0.32
A92-727017	91.2	2.6	-8.15	112.1	0.35
IA2007R	94.7	2.4	-8.18	114.7	0.43
Kenwood 94	106.0	2.5	-8.28	126.9	0.49
Probst	101.0	2.4	-8.75	122.2	0.51
CX329	89.0	2.6	-9.17	112.5	0.51
P9272	99.5	2.8	-9.33	125.4	0.52
S19-90	100.6	2.4	-9.48	123.3	0.51
IA2008R	101.6	2.7	-9.69	127.8	0.54
P9273	100.7	2.8	-9.79	128.2	0.54
S24-92	113.3	2.4	-10.14	137.2	0.56
Sturdy	98.5	2.7	-10.33	126.7	0.38
S28-01	104.9	2.6	-10.63	132.5	0.40
BSR101	102.7	2.7	-10.90	131.9	0.61
LSD(0.05)	9.6	NS‡	1.92		

† RY = (individual plot yield÷experiment mean yield)×100.
‡ NS = not significant.

Table 12. Results of linear regression analysis of relative plant height† (RH) versus log_{10}-transformed final SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1995 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RH	$Log_{10}(Pf+1)$	Slope	Y intercept	R^2
IA2007R	98.3	2.4	-1.31 NS	101.7	0.05
Jack	119.7	1.7	-1.64 NS	122.7	0.08
AP3035	94.3	2.4	-1.77 NS	98.6	0.10
CX366	116.9	2.5	-1.90 *	121.7	0.12
IA2022	108.1	2.2	-2.51 *	113.8	0.16
P9303	95.5	2.5	-2.64 **	102.0	0.26
Kenwood 94	99.1	2.5	-2.73 *	106.0	0.19
CX329	103.0	2.6	-2.78 **	110.1	0.25
A92-727017	107.5	2.6	-2.83 **	114.7	0.29
P9381	101.1	2.3	-2.91 *	108.2	0.18
CX298	99.3	2.6	-3.15 **	107.6	0.36
Probst	104.6	2.4	-3.27 **	112.6	0.45
IA2008R	106.1	2.7	-3.90 **	116.7	0.26
S28-01	89.5	2.6	-3.98 **	100.0	0.25
S24-92	88.1	2.4	-4.02 **	97.7	0.35
Sturdy	96.8	2.7	-4.02 **	107.7	0.20
P9272	94.9	2.8	-4.42 **	107.1	0.52
S19-90	89.6	2.4	-4.72 **	101.0	0.35
P9273	88.6	2.8	-4.75 **	101.9	0.48
BSR101	96.6	2.7	-4.89 **	109.9	0.32
LSD(0.05)	4.9	NS‡	1.27		

*, ** significant at the 0.05 and 0.01 probability level, respectively.
† RH = (individual plot height÷experiment mean height)×100.
‡ NS = not significant.

Table 13. Results of linear regression analysis of relative seed weight† (RW) versus log_{10}-transformed final SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1995 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RW	$Log_{10}(Pf+1)$	Slope	Y intercept	R^2
AP3035	98.9	2.4	-0.98 NS	101.4	0.08
P9303	107.3	2.5	-1.37 NS	110.8	0.10
IA2007R	105.5	2.4	-1.64 *	109.8	0.15
Jack	89.8	1.7	-1.83 *	93.1	0.14
S24-92	100.8	2.4	-1.84 **	105.3	0.24
IA2022	97.6	2.2	-1.96 **	102.1	0.28
P9272	100.9	2.8	-1.96 **	106.5	0.21
S28-01	92.6	2.6	-2.08 **	98.0	0.23
S19-90	120.8	2.4	-3.27 **	128.7	0.33
CX366	96.5	2.5	-2.36 **	102.2	0.21
Kenwood 94	97.3	2.5	-2.38 **	103.1	0.36
P9381	90.8	2.3	-2.41 **	96.4	0.28
IA2008R	97.6	2.7	-2.50 **	104.5	0.29
A92-727017	111.5	2.6	-2.58 NS	118.2	0.00
Probst	95.6	2.4	-2.63 **	102.0	0.27
CX329	90.5	2.6	-2.92 **	97.9	0.41
Sturdy	126.2	2.7	-3.07 NS	134.6	0.00
P9273	95.1	2.8	-3.28 **	104.2	0.41
CX298	98.8	2.6	-3.85 **	108.6	0.32
BSR101	110.3	2.7	-4.60 **	122.5	0.46
LSD(0.05)	15.3	NS‡	4.39		

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Seed weight = g 100^{-1} $seeds^{-1}$; RW = (individual plot seed weight÷experiment mean seed weight)×100.

‡ NS = not significant.

Table 14. Initial SCN population densities for the 1996 field experiment, by genotype and location.

	Noninfested†			Infested			
Genotype	Ames	Kanawha	Mean	Ames	Kanawha	Napier	Mean
A92-727017	0	13	7	6963	1631	13 750	7448
AP3035	0	0	0	4775	1038	15 388	7067
BSR101	0	69	35	6450	1863	15 288	7867
CX298	0	19	10	6200	831	12 700	6577
CX329	0	13	7	5687	2300	11 813	6600
CX366	0	0	0	4488	2063	12 150	6233
IA2007R	0	0	0	6063	1775	12 875	6904
IA2008R	0	69	35	5687	1988	14 688	7454
IA2022	0	6	3	2450	1206	9 475	4377
Jack	0	0	0	5200	2863	11 150	6404
Kenwood 94	0	0	0	4250	944	10 750	5315
P9272	0	88	44	4838	1763	13 925	6842
P9273	0	69	35	5475	1806	11 563	6281
P9303	0	31	16	5225	1088	11 625	5979
P9381	0	6	3	3944	2044	13 663	6550
Probst	0	0	0	4875	1131	18 175	8060
S19-90	0	38	19	5200	1800	13 550	6850
S24-92	0	13	7	5275	1400	18 563	8413
S28-01	0	38	19	4888	1481	14 038	6802
Sturdy	21	25	23	3625	1625	14 038	6429
Mean	1	25	13	5078	1632	1346	2685
LSD(0.05)	NS‡	NS	NS	NS	NS	NS	NS

Values presented are eggs 100^{-1} cm^{-3} soil and are means of eight replications per location.

† Noninfested locations had several plots with detectable SCN population densities.

‡ NS = not significant.

Table 15. Final SCN population densities for the 1996 field experiment, by genotype and location.

	Noninfested†			Infested			
Genotype	Ames	Kanawha	Mean	Ames	Kanawha	Napier	Mean
A92-727017	75	438	257	4113	3038	5050	4067
AP3035	13	1213	613	3163	2738	5525	3868
BSR101	38	825	432	2625	1913	3900	2813
CX298	0	388	194	4038	2150	4875	3688
CX329	0	613	307	4150	3575	4100	3942
CX366	63	688	376	3163	2700	4825	3563
IA2007R	96	613	355	3850	3200	4113	3721
IA2008R	210	588	399	4138	3025	4050	3738
IA2022	188	425	307	3463	2325	5825	3871
Jack	0	25	13	875	838	913	875
Kenwood 94	0	625	313	2313	2775	3225	2771
P9272	13	925	469	3138	3125	4975	3746
P9273	10	200	105	3412	3363	6000	4258
P9303	0	775	388	4088	2775	6325	4396
P9381	0	375	188	3725	3325	3813	3621
Probst	13	463	238	3513	3700	5775	4329
S19-90	0	925	463	2463	2050	3425	2646
S24-92	38	200	119	5275	2350	3800	3233
S28-01	25	775	400	4888	3437	5213	3508
Sturdy	53	325	189	3625	2150	4900	3129
Mean	42	570	306	3501	2728	4531	3587
LSD(0.05)	NS‡	NS	NS	1746	1399	2381	1209

Values presented are eggs 100^{-1} cm^{-3} soil and are means of eight replications per location.
† Noninfested locations had several plots with detectable SCN population densities.
‡ NS = not significant.

Table 16. Reproductive factors† for soybean genotypes included in the 1996 field experiment, by genotype and location.

	Noninfested‡			Infested			
Genotype	Ames	Kanawha	Mean	Ames	Kanawha	Napier	Mean
A92-727017	NA§	7.1	NA	0.6	2.3	0.4	1.1
AP3035	NA	NA	NA	0.9	8.0	0.4	2.9
BSR101	NA	9.5	NA	0.4	9.0	0.3	3.2
CX298	NA	12.9	NA	1.1	3.6	0.4	1.7
CX329	NA	32.5	NA	0.8	3.3	0.4	1.5
CX366	NA	NA	NA	1.1	12.0	0.5	4.5
IA2007R	NA	NA	NA	0.9	3.5	0.5	1.6
IA2008R	NA	8.1	NA	1.0	2.1	0.3	1.1
IA2022	NA	50.1	NA	1.6	3.1	0.7	1.8
Jack	NA	NA	NA	0.2	0.9	0.1	0.4
Kenwood 94	NA	NA	NA	0.6	5.0	0.5	1.9
P9272	NA	8.3	NA	0.7	5.6	0.4	2.2
P9273	NA	4.2	NA	0.8	3.0	0.5	1.4
P9303	NA	3.1	NA	1.1	2.0	1.2	1.4
P9381	NA	25.8	NA	1.2	2.5	0.3	1.3
Probst	NA	NA	NA	0.8	8.5	0.5	3.2
S19-90	NA	6.5	NA	0.8	4.1	0.3	1.7
S24-92	NA	5.9	NA	0.8	4.0	0.2	1.7
S28-01	NA	16.9	NA	0.4	3.3	0.4	1.4
Sturdy	0.7	0.2	0.5	0.7	3.1	0.4	1.4
Mean	0.0	10.0	5.0	0.8	4.5	0.4	1.9
LSD(0.05)	NS¶	7.6	NS	NS	NS	0.4	NS

Values presented are means of eight replications per location.

† Reproductive factor = final SCN egg population density÷initial SCN egg population density.

‡ Noninfested locations had several plots with detectable SCN population densities.

§ NA = not applicable; zero detectable initial SCN population density.

¶ NS = not significant.

Table 17. Yield of soybean genotypes included in the 1996 field experiment, by genotype and location.

	Noninfested				Infested				
Genotype	Ames	Kanawha	Mean	Rank	Ames	Kanawha	Napier	Mean	Rank
A92-727017	4515	3605	4060	17	3076	2364	3135	2858	16
AP3035	4957	4358	4658	2	3536	3288	2832	3219	6
BSR101	4463	4117	4290	14	3231	3168	2378	2926	11
CX298	4377	3567	3972	18	3260	2351	2828	2813	18
CX329	4254	3522	3888	19	2989	2207	2791	2662	19
CX366	4328	3345	3836	20	3049	1865	2914	2609	20
IA2007R	4823	4263	4524	9	3197	2938	2427	2854	17
IA2008R	4551	4157	4341	13	3663	3274	2856	3264	5
IA2022	4576	4214	4395	11	3764	3170	3033	3322	2
Jack	4588	4150	4369	12	4187	3069	3747	3667	1
Kenwood 94	4606	4346	4476	10	3484	2986	2684	3051	9
P9272	4578	4513	4546	7	3132	3206	2284	2874	14
P9273	4631	4534	4580	6	3472	3338	2987	3266	4
P9303	4776	4300	4538	8	3533	2665	2466	2888	13
P9381	4695	3832	4264	15	3580	2661	2666	2969	10
Probst	4538	3887	4213	16	3384	2729	3047	3053	8
S19-90	4800	4420	4610	3	3062	3223	2424	2903	12
S24-92	4830	4740	4785	1	3725	3683	2539	3316	3
S28-01	4828	4367	4598	5	3691	2575	2920	3062	7
Sturdy	4652	4561	4603	4	2894	2980	2719	2864	15
Mean	4618	4140	4379		3395	2887	2784	3022	
LSD(0.05)	254	196	161		295	267	319	275	

Values presented are kg ha^{-1} and are means of eight replications per genotype.

Table 18. Tolerance indices† (TI) and results of linear regression analysis of relative yield‡ (RY) versus log_{10}-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pi+1)$] for the 1996 field experiment. Genotypes are listed in decreasing value for slope.

	Mean						
Genotype	RY	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2	TI	TI rank
Jack	110.8	2.1	-4.79	121.1	0.28	83.9	1
Probst	98.7	2.1	-7.91	115.6	0.55	72.5	4
IA2008R	103.2	2.3	-8.16	122.1	0.64	75.0	3
CX298	92.0	2.2	-8.30	110.3	0.48	69.6	7
A92-727017	93.7	2.3	-8.35	112.6	0.53	70.0	6
CX366	87.0	2.1	-8.42	105.1	0.42	68.0	12
IA2022	105.3	2.1	-8.84	123.8	0.70	75.4	2
CX329	88.5	2.3	-9.14	109.3	0.60	67.4	13
P9381	97.9	2.2	-10.14	120.2	0.62	68.8	10
Kenwood 94	101.7	2.0	-10.17	122.1	0.64	68.2	11
P9273	105.8	2.4	-10.57	131.1	0.82	70.5	5
AP3035	106.5	2.0	-10.64	128.3	0.73	69.0	9
BSR101	97.5	2.4	-11.37	124.6	0.76	67.0	14
P9303	99.6	2.1	-11.39	123.5	0.57	63.2	16
S28-01	103.2	2.3	-11.58	130.1	0.64	65.7	15
IA2007R	98.1	2.1	-12.00	123.8	0.74	63.1	17
S24-92	109.6	2.3	-12.28	137.3	0.77	69.5	8
Sturdy	99.2	2.3	-13.26	129.8	0.82	62.3	20
P9272	99.5	2.4	-13.62	131.8	0.76	63.0	18
S19-90	100.7	2.2	-13.66	131.4	0.84	62.7	19
LSD(0.05)	10.0	NS§	2.76				

† TI = (mean relative yield in SCN-infested fields÷mean relative yield in noninfested fields)×100.
‡ RY = (individual plot yield÷experiment mean yield)×100.
§ NS = not significant.

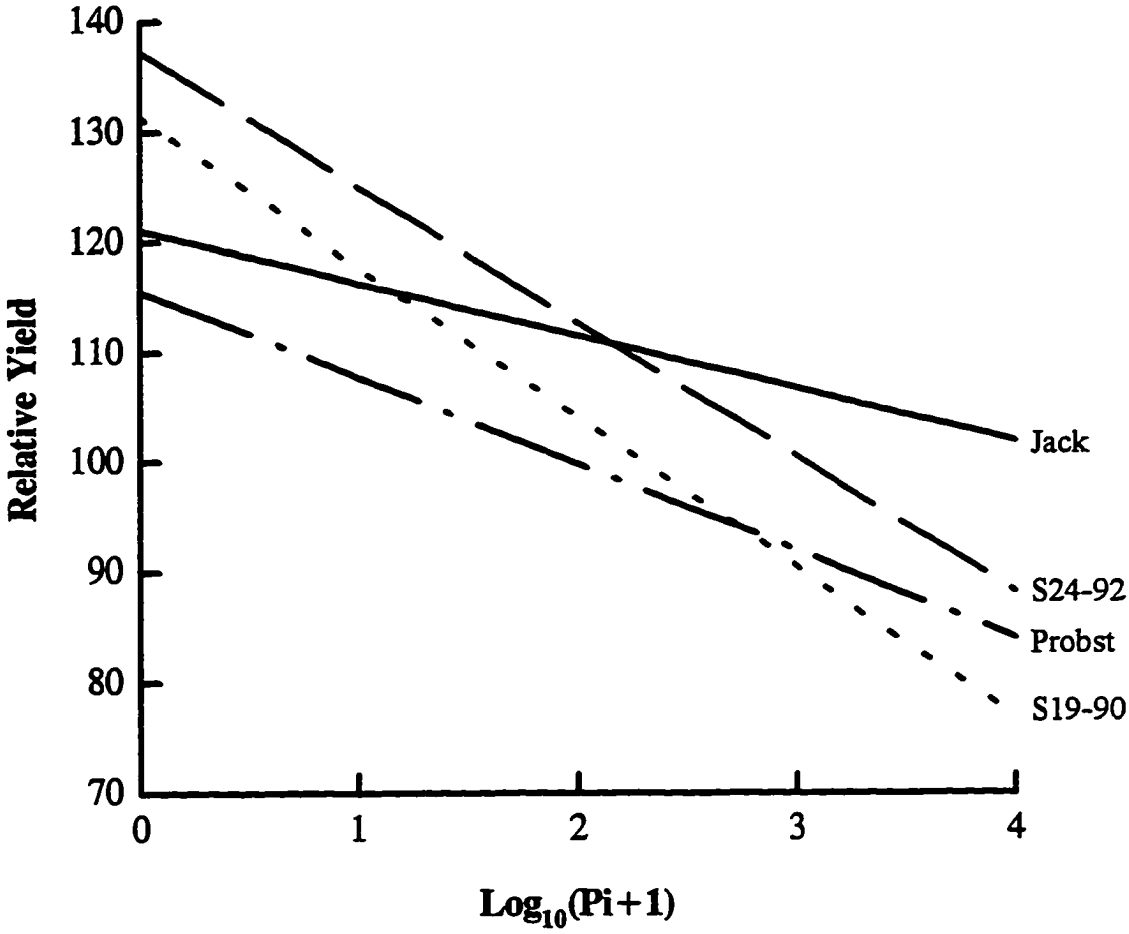

Fig. 2. Linear regression lines of relative yield [(individual plot yield÷experiment mean yield)×100] versus $\log_{10}$-transformed initial SCN egg population densities [Log_{10}(Pi+1)] for SCN-resistant 'Jack' (Y=121.1 - 4.79 X), putative tolerant 'Probst' (Y=115.6 - 7.91X), putative moderately tolerant 'S24-92' (Y=137.3 - 12.28X), and putative intolerant 'S19-90' (Y=131.4 - 13.66X) for the 1996 field experiment.

Table 19. Results of linear regression analysis of relative plant height† (RH) versus log_{10}-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1996 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RH	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2
Jack	121.6	2.1	-4.39	131.0	0.51
P9272	87.6	2.4	-5.37	100.4	0.54
P9273	89.1	2.4	-5.50	102.3	0.62
Probst	106.7	2.1	-5.85	119.2	0.60
CX366	117.3	2.1	-5.87	129.8	0.62
A92-727017	108.1	2.3	-6.08	121.9	0.59
S24-92	88.2	2.3	-6.20	102.2	0.66
IA2008R	106.7	2.3	-6.46	121.6	0.59
IA2022	113.2	2.1	-6.48	126.7	0.66
AP3035	98.6	2.0	-6.55	112.1	0.74
CX298	99.9	2.2	-6.58	114.1	0.53
Kenwood 94	101.5	2.0	-6.89	115.3	0.58
P9381	100.2	2.2	-7.23	116.1	0.66
CX329	103.1	2.3	-7.36	119.9	0.68
Sturdy	95.3	2.3	-7.80	113.3	0.64
P9303	96.2	2.1	-7.95	112.9	0.65
IA2007R	99.2	2.1	-8.12	116.5	0.72
S19-90	86.4	2.2	-8.16	104.7	0.76
S28-01	87.5	2.3	-8.18	106.5	0.78
BSR101	93.9	2.4	-8.90	115.1	0.73
LSD(0.05)	14.9	NS‡	1.16		

† RH = (individual plot height÷experiment mean height)×100.
‡ NS = not significant.

Table 20. Results of linear regression analysis of relative seed weight† (RW) versus log_{10}-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pi+1)$] for the 1996 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RW	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2
Jack	91.9	2.1	-1.96	96.2	0.14
AP3035	103.7	2.0	-2.46	108.7	0.28
Kenwood 94	100.4	2.0	-2.48	105.4	0.32
S24-92	98.3	2.3	-2.51	104.0	0.47
BSR101	107.3	2.4	-2.52	113.3	0.34
IA2008R	93.4	2.3	-2.83	99.9	0.34
IA2022	93.3	2.1	-2.92	99.4	0.44
P9273	97.0	2.4	-3.19	104.6	0.54
Probst	97.1	2.1	-3.19	103.9	0.39
P9303	105.5	2.1	-3.33	112.5	0.25
S19-90	130.5	2.2	-3.33	138.0	0.41
S28-01	93.6	2.3	-3.50	101.7	0.32
P9272	107.9	2.4	-3.56	116.4	0.58
A92-727017	90.5	2.3	-3.60	98.7	0.25
CX366	93.2	2.1	-3.60	100.9	0.30
P9381	88.2	2.2	-3.63	96.2	0.33
CX329	92.8	2.3	-3.70	101.2	0.42
CX298	100.5	2.2	-4.15	109.7	0.33
IA2007R	107.4	2.1	-4.39	116.9	0.47
Sturdy	112.3	2.3	-4.89	123.6	0.61
LSD(0.05)	9.8	NS‡	1.26		

† Seed weight = g 100^{-1} $seeds^{-1}$; RW = (individual plot seed weight÷experiment mean seed weight)×100.

‡ NS = not significant.

Table 21. Results of linear regression analysis of relative yield† (RY) versus log_{10}-transformed final SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1996 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RY	$Log_{10}(Pf+1)$	Slope	Y intercept	R^2
Jack	110.8	1.7	-5.81	120.5	0.25
IA2008R	103.2	2.6	-8.40	125.1	0.45
IA2022	105.3	2.4	-8.49	125.8	0.54
P9381	97.9	2.3	-9.74	120.7	0.46
CX366	87.0	2.5	-10.08	112.5	0.39
CX329	88.5	2.4	-10.09	112.5	0.60
A92-727017	93.7	2.5	-10.25	119.4	0.55
Probst	98.7	2.6	-10.36	125.5	0.62
CX298	92.0	2.4	-10.43	117.2	0.60
P9273	105.8	2.4	-10.61	131.7	0.73
Kenwood 94	101.7	2.5	-11.42	129.7	0.54
IA2007R	98.1	2.4	-12.01	127.1	0.58
S24-92	109.6	2.6	-12.41	141.3	0.47
AP3035	106.5	2.5	-12.50	138.3	0.64
S28-01	103.2	2.4	-12.69	134.3	0.59
P9303	99.6	2.5	-12.94	131.7	0.59
P9272	99.5	2.5	-13.04	132.2	0.57
BSR101	97.5	2.6	-13.11	131.0	0.58
Sturdy	99.2	2.6	-13.76	134.3	0.57
S19-90	100.7	2.5	-14.85	137.1	0.63
LSD(0.05)	10.0	0.7	3.66		

† RY = (individual plot yield÷experiment mean yield)×100.

Table 22. Results of linear regression analysis of relative plant height† (RH) versus log_{10}-transformed final SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1996 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RH	$Log_{10}(Pf+1)$	Slope	Y intercept	R^2
Jack	121.6	1.7	-4.63	129.3	0.34
P9272	87.6	2.5	-4.85	99.8	0.36
P9381	100.2	2.3	-4.99	111.8	0.25
P9273	89.1	2.4	-5.11	101.6	0.48
Probst	106.7	2.6	-5.17	120.1	0.31
S24-92	88.2	2.6	-5.86	103.2	0.35
IA2022	113.2	2.4	-5.88	127.3	0.46
CX366	117.3	2.5	-5.94	132.3	0.40
Kenwood 94	101.5	2.5	-6.25	116.8	0.32
A92-727017	108.1	2.5	-6.31	123.9	0.45
IA2007R	99.2	2.4	-6.42	114.6	0.35
IA2008R	106.7	2.6	-6.49	123.5	0.40
CX329	103.1	2.4	-6.61	118.9	0.46
CX298	99.9	2.4	-6.76	116.2	0.44
P9303	96.2	2.5	-7.31	114.4	0.44
AP3035	98.6	2.5	-7.55	117.8	0.63
S19-90	86.4	2.5	-7.89	105.7	0.45
S28-01	87.5	2.4	-8.19	107.6	0.59
Sturdy	95.3	2.6	-8.55	117.1	0.50
BSR101	93.9	2.6	-9.35	117.8	0.46
LSD(0.05)	6.7	0.7	1.54		

† RH = (individual plot height÷experiment mean height)×100.

Table 23. Results of linear regression analysis of relative seed weight† (RW) versus log_{10}-transformed final SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pf+1)$] for the 1996 field experiment. Genotypes are listed in decreasing value for slope.

	Mean				
Genotype	RW	$Log_{10}(Pf+1)$	Slope	Y intercept	R^2
Jack	91.9	1.7	-2.53	96.2	0.14
S24-92	98.3	2.6	-2.87	105.7	0.36
IA2022	93.3	2.4	-2.88	100.3	0.36
P9272	107.9	2.5	-3.38	116.4	0.43
P9273	97.0	2.4	-3.47	105.5	0.57
IA2008R	93.4	2.6	-3.58	102.7	0.37
S19-90	130.5	2.5	-3.58	139.3	0.30
Kenwood 94	100.4	2.5	-3.68	109.4	0.47
BSR101	107.3	2.6	-4.08	117.7	0.52
S28-01	93.6	2.4	-4.27	104.0	0.36
AP3035	103.7	2.5	-4.30	114.6	0.54
CX329	92.8	2.4	-4.39	103.2	0.49
P9381	88.2	2.3	-4.49	98.7	0.41
CX366	93.2	2.5	-4.57	104.8	0.31
Probst	97.1	2.6	-4.63	109.1	0.54
IA2007R	107.4	2.4	-4.81	119.1	0.44
A92-727017	90.5	2.5	-5.34	103.8	0.38
P9303	105.5	2.5	-5.40	118.9	0.52
CX298	100.5	2.4	-5.88	114.7	0.53
Sturdy	112.3	2.6	-5.89	127.4	0.56
LSD(0.05)	4.4	0.7	1.67		

† Seed weight = g 100^{-1} $seeds^{-1}$; RW = (individual plot seed weight÷experiment mean seed weight)×100.

Table 24. Tolerance indices† (TI) and results of linear regression analysis of relative yield‡ (RY) versus $\log_{10}$-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil + 1; $Log_{10}(Pi+1)$] for the 1995 and 1996 field experiments combined. Genotypes are listed in decreasing value for slope.

	Mean						
Genotype	RY	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2	TI	TI rank
Jack	117.0	2.1	-4.92	127.4	0.19	85.3	1
CX366	93.4	2.0	-8.17	110.1	0.37	72.0	6
Probst	106.5	2.0	-8.51	123.7	0.43	73.6	3
CX298	96.9	2.1	-8.88	115.4	0.47	71.6	8
IA2022	111.5	2.0	-9.49	130.4	0.56	75.2	2
A92-727017	100.4	2.2	-9.51	121.0	0.52	70.3	11
IA2008R	109.8	2.3	-9.92	132.3	0.54	73.0	4
P9381	103.9	2.3	-10.30	127.6	0.40	71.7	7
AP3035	111.7	2.0	-10.56	132.8	0.62	71.1	10
CX329	94.8	2.1	-10.64	117.0	0.62	67.7	16
P9273	110.6	2.4	-10.70	135.9	0.57	71.3	9
Kenwood 94	110.9	2.0	-10.80	132.5	0.58	70.2	12
P9303	106.1	2.1	-10.87	129.0	0.51	68.5	14
S28-01	111.2	2.3	-11.98	139.3	0.42	70.1	13
IA2007R	103.1	2.1	-12.35	129.0	0.64	66.0	19
S19-90	107.9	2.2	-12.40	134.9	0.64	67.7	17
S24-92	118.8	2.1	-12.45	145.5	0.62	72.3	5
BSR101	107.1	2.3	-12.45	135.8	0.66	67.9	15
P9272	106.6	2.4	-13.24	137.9	0.62	67.4	18
Sturdy	107.5	2.2	-13.83	137.8	0.70	65.0	20
LSD(0.05)	7.6	NS	1.32			5.6	

† TI = (mean relative yield in SCN-infested fields÷mean relative yield in noninfested fields)×100.
‡ RY = (individual plot yield÷experiment mean yield)×100.
§ NS = not significant.

Table 25. Days after planting to R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) at the Ames SCN-infested and noninfested locations for the 1995 and 1996 field experiments combined.

	DAPR1			DAPR8			TOTALR		
Genotype	Non	Inf		Non	Inf		Non	Inf	
A92-727017	57	56	NS§	131	132	*	74	76	NS
AP3035	45	46	*	128	128	NS	83	83	NS
BSR101	46	46	NS	120	120	NS	74	74	NS
CX298	49	51	NS	130	130	NS	80	79	NS
CX329	49	51	*	131	130	NS	82	79	*
CX366	51	53	*	132	133	NS	81	80	NS
IA2007R	49	50	NS	127	127	NS	78	77	NS
IA2008R	48	49	NS	122	123	*	74	74	NS
IA2022	46	48	NS	127	126	NS	81	79	*
Jack	48	49	NS	128	129	*	80	80	NS
Kenwood 94	48	49	NS	122	123	NS	74	74	NS
P9272	44	46	*	122	123	*	78	77	NS
P9273	45	47	*	121	122	*	77	76	NS
P9303	47	48	NS	126	126	NS	80	78	NS
P9381	51	56	*	133	133	NS	82	77	*
Probst	48	51	*	138	132	NS	84	81	*
S19-90	45	47	*	119	119	NS	74	73	*
S24-92	46	47	*	120	121	*	74	74	NS
S28-01	49	52	*	127	121	*	78	73	*
Sturdy	44	46	*	121	118	*	77	73	*

* significant at the 0.05 probability level.

† R1 = beginning bloom; R8 = harvest maturity (Fehr et al., 1971).

‡ Non = noninfested; Inf = SCN-infested.

§ NS = not significant.

Table 26. Final number of nodes (Node), plant height (Hgt; mm), shoot dry weight (Sdw; g), root dry weight (Rdw; g), shoot:root dry weight ratio (S:R), final SCN population densities† (Pf), and reproductive factors‡ (Rf) for six levels of initial SCN population density (Pi) in an eight week greenhouse experiment.

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
A92-727017	0	10	197	2.67	1.90	1.39	0	—
	100	9	175	2.14	1.60	1.24	580	5.8
	500	9	180	2.06	1.55	1.32	3 020	6.0
	1000	9	171	2.02	1.52	1.24	11 500	11.5
	2000	10	170	1.80	1.41	1.24	24 080	12.0
	4000	9	173	1.60	1.48	1.01	11 960	3.0
	LSD(0.05)	NS§	NS	NS	NS	NS	17 301	NS
AP3035	0	9	196	3.25	1.95	1.64	0	—
	100	9	164	2.27	1.59	1.43	1 240	12.4
	500	9	160	2.00	1.33	1.47	3 640	7.3
	1000	9	175	2.51	1.67	1.48	8 240	8.2
	2000	9	160	2.12	1.40	1.50	17 220	8.6
	4000	8	143	1.13	0.95	1.15	24 300	6.1
	LSD(0.05)	NS	28.1	0.73	0.41	0.29	13 872	NS
BSR101	0	10	202	2.72	1.70	1.59	0	—
	100	9	183	2.51	1.61	1.52	1 240	12.4
	500	10	186	2.49	1.65	1.49	4 640	9.3
	1000	10	181	2.10	1.44	1.41	9 500	9.5
	2000	9	171	1.55	1.14	1.39	8 740	4.4
	4000	10	216	1.51	0.96	1.56	16 940	4.2
	LSD(0.05)	NS	NS	NS	NS	NS	12 018	NS

Table 26 (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
CX298	0	10	196	2.75	1.73	1.58	0	—
	100	9	183	2.16	1.42	1.50	560	5.6
	500	9	186	2.00	1.32	1.51	8 400	16.8
	1000	10	207	1.94	1.14	1.77	5 360	5.4
	2000	10	212	1.50	1.02	1.50	11 600	5.8
	4000	9	192	0.91	0.70	1.33	16 060	4.0
	LSD(0.05)	NS	NS	0.96	0.50	NS	8732	NS
CX329	0	10	183	2.38	1.65	1.44	0	—
	100	9	157	2.18	1.51	1.39	1 240	12.4
	500	9	150	1.69	1.29	1.31	2 880	5.8
	1000	9	157	1.91	1.36	1.39	18 100	18.1
	2000	9	174	1.79	1.31	1.44	15 640	7.8
	4000	8	137	0.90	0.87	1.03	11 240	2.8
	LSD(0.05)	NS	32	NS	NS	NS	NS	NS
CX366	0	10	239	2.98	1.70	1.69	0	—
	100	9	216	2.46	1.57	1.54	1 100	11.0
	500	9	235	2.14	1.45	1.45	3 700	7.4
	1000	9	252	2.40	1.70	1.43	13 240	13.2
	2000	9	235	2.12	1.26	1.72	13 740	6.9
	4000	9	206	1.34	1.00	1.28	8 040	2.0
	LSD(0.05)	NS	NS	NS	NS	NS	9563	NS

Table 26 (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
IA2007R	0	10	169	2.72	1.68	1.57	0	—
	100	10	160	2.55	1.79	1.40	460	4.6
	500	10	160	2.87	1.65	1.77	4 340	8.7
	1000	9	150	2.57	1.86	1.35	14 840	14.8
	2000	10	145	2.17	1.41	1.52	20 500	10.3
	4000	9	140	1.44	1.08	1.30	20 460	5.1
	LSD(0.05)	NS	29	0.80	0.45	NS	16 922	NS
IA2008R	0	9	214	2.52	1.45	1.63	0	—
	100	10	239	2.30	1.24	1.89	1 320	13.2
	500	9	172	1.82	1.23	1.46	4 540	9.1
	1000	9	167	1.62	1.24	1.28	17 480	17.5
	2000	9	204	1.98	1.25	1.46	26 080	13.0
	4000	10	218	2.07	1.46	1.32	21 260	5.3
	LSD(0.05)	NS	NS	NS	NS	NS	NS	NS
IA2022	0	8	209	2.22	1.44	1.54	0	—
	100	9	221	2.26	1.54	1.42	300	3.0
	500	9	203	1.88	1.31	1.42	4 760	9.5
	1000	10	205	2.03	1.32	1.62	6 960	7.0
	2000	9	208	1.58	1.29	1.25	9 480	4.7
	4000	9	175	1.39	1.06	1.28	16 880	4.2
	LSD(0.05)	NS	NS	0.72	0.38	NS	9641	NS

Table 26 (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
Jack	0	10	194	2.64	1.90	1.38	0	—
	100	10	174	2.36	1.62	1.39	260	2.6
	500	10	209	3.15	0.92	1.58	300	0.6
	1000	9	160	1.75	0.34	1.34	400	0.4
	2000	10	187	2.42	1.62	1.46	940	0.5
	4000	9	141	1.31	1.20	1.05	740	0.2
	LSD(0.05)	NS	33	1.04	0.57	0.37	NS	NS
Kenwood 94	0	9	207	2.31	1.70	1.34	0	—
	100	8	210	2.88	2.15	1.35	780	7.8
	500	10	206	2.21	1.60	1.39	7 480	15.0
	1000	9	178	2.03	1.73	1.12	7 800	7.8
	2000	10	191	1.59	1.34	1.14	9 860	4.9
	4000	9	176	1.66	1.34	1.12	20 900	5.2
	LSD(0.05)	NS	NS	NS	NS	NS	11 654	NS
P9272	0	5	129	2.07	1.04	1.97	0	—
	100	6	136	2.43	1.11	2.17	640	6.4
	500	6	147	2.64	1.22	2.04	10 520	21.0
	1000	6	133	1.98	0.95	2.04	19 520	19.5
	2000	6	127	1.77	0.97	1.84	16 860	8.4
	4000	6	137	1.15	0.86	1.42	27 860	7.0
	LSD(0.05)	NS	NS	1.01	NS	0.47	NS	NS

Table 26 (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
P9273	0	8	197	2.79	1.47	1.78	0	—
	100	7	168	2.09	1.20	1.78	240	2.4
	500	7	175	2.64	1.61	1.53	4 340	8.7
	1000	7	172	2.18	1.30	1.63	12 660	12.7
	2000	8	178	2.08	1.33	1.67	19 580	9.8
	4000	8	159	1.15	0.90	1.26	8 580	2.1
	LSD(0.05)	NS	NS	NS	NS	NS	12 776	NS
P9303	0	7	184	2.61	1.44	1.80	0	—
	100	8	184	2.54	1.52	1.66	200	2.0
	500	9	190	2.34	1.49	1.51	2 580	5.2
	1000	7	161	1.83	1.21	1.49	12 760	12.8
	2000	9	175	2.16	1.55	1.36	11 020	5.5
	4000	8	174	1.49	1.25	1.22	12 820	3.2
	LSD(0.05)	NS	NS	NS	NS	NS	NS	NS
P9381	0	10	213	2.24	1.41	1.57	0	—
	100	10	225	2.53	1.51	1.67	980	9.8
	500	10	220	1.81	1.12	1.57	2 660	5.3
	1000	10	211	2.29	1.49	1.60	9 080	9.1
	2000	10	218	1.70	1.03	1.64	4 760	2.4
	4000	10	183	1.26	0.74	1.88	12 340	3.1
	LSD(0.05)	NS	NS	NS	NS	NS	6906	NS

Table 26 (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
Probst	0	10	222	2.59	1.70	1.52	0	—
	100	10	225	2.50	1.48	1.68	1 120	11.2
	500	9	192	1.78	1.33	1.26	5 780	11.6
	1000	10	201	2.30	1.49	1.54	8 800	8.8
	2000	10	207	1.68	1.22	1.38	12 160	6.1
	4000	9	173	0.78	0.65	1.16	16 400	4.1
	LSD(0.05)	NS	NS	1.04	0.54	NS	7512	NS
S19-90	0	7	211	2.53	1.55	1.57	0	—
	100	7	194	3.49	1.83	1.93	1 520	15.2
	500	8	175	1.97	1.32	1.48	3 240	6.5
	1000	7	209	2.34	1.69	1.43	11 740	11.7
	2000	7	173	2.05	1.37	1.49	32 140	16.1
	4000	7	168	1.64	1.17	1.41	35 180	8.8
	LSD(0.05)	NS	38	0.84	0.45	0.29	24 266	NS
S24-92	0	7	182	2.51	1.45	1.77	0	—
	100	6	188	2.67	1.27	2.02	940	9.4
	500	6	189	2.50	1.30	1.92	3 700	7.4
	1000	7	190	2.46	1.33	1.81	6 640	6.6
	2000	6	172	1.95	1.20	1.52	10 400	5.2
	4000	7	182	1.64	1.09	1.51	29 000	7.3
	LSD(0.05)	NS	63	NS	NS	0.41	18 246	NS

Table 26 (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
S28-01	0	5	140	3.35	1.61	2.11	0	—
	100	6	104	2.26	1.17	1.93	500	5.0
	500	6	108	2.25	1.21	1.90	1 780	3.6
	1000	6	113	1.50	0.92	1.68	5 900	5.9
	2000	6	111	1.63	0.95	1.73	8 920	4.5
	4000	6	137	2.09	1.39	1.51	26 460	6.6
	LSD(0.05)	NS	NS	0.88	0.44	NS	NS	NS
Sturdy	0	9	194	2.39	1.81	1.29	0	—
	100	9	216	3.09	2.06	1.47	760	7.6
	500	9	175	2.41	1.69	1.65	4 060	8.1
	1000	9	191	2.61	1.86	1.40	20 620	20.6
	2000	9	180	1.97	1.43	1.30	24 820	12.4
	4000	8	160	1.56	1.20	1.30	8 540	2.1
	LSD(0.05)	NS	NS	NS	NS	NS	NS	NS

Values presented are means of five replications.
† SCN population densities expressed as eggs 100^{-1} cm^{-3} potting mix.
‡ Rf = Pf÷Pi.
§ NS = not significant.

Table 27. Results of linear regression analysis of plant height (Height) and shoot dry weight versus initial SCN population density (eggs 100^{-1} cm^{-3} potting mix) in an eight week greenhouse experiment.

	Height (mm)			Shoot dry weight (g)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2
A92-727917	-0.0034 NS†	181.9	0.02	-0.00020 NS	2.3	0.08
AP3035	-0.0086 *	177.2	0.15	-0.00037 **	2.7	0.27
BSR101	0.0047 NS	183.9	0.04	-0.00031 **	2.5	0.23
CX298	0.0018 NS	193.9	0.00	-0.00038 **	2.4	0.37
CX329	-0.0061 NS	167.4	0.08	-0.00031 **	2.2	0.29
CX366	-0.0056 NS	237.6	0.02	-0.00032 *	2.6	0.21
IA2007R	-0.0064 NS	162.2	0.09	-0.00033 *	2.8	0.19
IA2008R	0.0016 NS	200.3	0.00	-0.00005 NS	2.1	0.00
IA2022	-0.0089 NS	214.6	0.07	0.00021 NS	2.2	0.13
Jack	-0.0111 *	191.6	0.15	-0.00031 NS	2.7	0.13
Kenwood 94	-0.0078 NS	204.5	0.07	-0.00024 NS	2.4	0.13
P9272	-0.0001 NS	135.0	0.00	-0.00031 *	2.4	0.19
P9273	-0.0051 NS	181.3	0.02	-0.00034 *	2.6	0.15
P9303	-0.0029 NS	181.7	0.01	-0.00025 *	2.5	0.15
P9381	-0.0082 NS	222.1	0.05	-0.00027 *	2.3	0.16
Probst	-0.0104 NS	216.7	0.10	-0.00041 **	2.5	0.36
S19-90	-0.0070 NS	195.4	0.07	-0.00029 *	2.7	0.17
S24-92	-0.0018 NS	185.9	0.00	-0.00025 *	2.6	0.14
S28-01	0.0039 NS	113.8	0.03	-0.00018 NS	2.4	0.07
Sturdy	-0.0097 NS	198.4	0.09	-0.00030 NS	2.7	0.13

*, ** significant at the 0.05 and 0.01 probability level, respectively.
† NS = not significant.

Table 28. Tolerance indices† (TI) of soybean genotypes for plant height at five initial SCN population densities (Pi) in an eight week greenhouse experiment.

	Pi (eggs 100^{-1} cm^{-3} soil)					
Genotype	100	500	1000	2000	4000	LSD(0.05)
A92-727017	93	94	89	89	88	NS‡
AP3035	85	84	92	83	73	16
BSR101	94	95	91	85	109	NS
CX298	95	96	106	107	99	NS
CX329	87	83	87	95	75	NS
CX366	95	107	118	104	95	NS
IA2007R	95	95	88	85	84	NS
IA2008R	119	87	81	92	108	NS
IA2022	112	103	102	102	86	NS
Jack	89	108	83	97	74	16
Kenwood 94	107	103	86	95	85	NS
P9272	107	116	107	101	110	NS
P9273	89	96	93	94	86	NS
P9303	108	105	91	98	97	NS
P9381	108	103	99	103	88	NS
Probst	106	87	94	97	80	NS
S19-90	99	85	97	84	82	NS
S24-92	114	115	117	105	109	NS
S28-01	76	79	83	81	99	NS
Sturdy	114	91	101	93	87	NS
LSD(0.05)	NS	NS	NS	NS	NS	

Values presented are means of five replications each.
† TI = (height in SCN-infested potting mix ÷ height in noninfested potting mix) × 100.
‡ NS = not significant.

Table 29. Tolerance indices† (TI) of soybean genotypes for shoot dry weight at five initial SCN population densities (Pi) in an eight week greenhouse experiment.

	Pi (eggs 100^{-1} cm^{-3} soil)					
Genotype	100	500	1000	2000	4000	LSD(0.05)
A92-727017	81	85	71	68	64	NS‡
AP3035	74	68	84	68	35	26
BSR101	100	97	75	58	58	NS
CX298	86	73	76	53	36	NS
CX329	95	73	90	76	40	NS
CX366	89	88	103	95	56	NS
IA2007R	96	114	101	85	63	32
IA2008R	106	99	75	74	10	NS
IA2022	126	89	107	94	74	NS
Jack	88	116	74	101	46	41
Kenwood 94	136	100	90	80	77	NS
P9272	122	128	112	95	59	NS
P9273	88	113	92	86	50	NS
P9303	135	109	76	87	72	NS
P9381	127	87	107	93	67	NS
Probst	105	66	115	77	37	NS
S19-90	157	95	108	96	71	NS
S24-92	123	117	115	97	71	NS
S28-01	67	68	46	50	63	NS
Sturdy	129	100	121	82	80	NS
LSD(0.05)	NS	NS	NS	NS	49	

Values presented are means of five replications each.

† TI = (shoot dry weight in SCN-infested potting mix ÷ shoot dry weight in noninfested potting mix) × 100.

‡ NS = not significant.

Table 30. Final number of nodes (Node), plant height (Hgt;mm), shoot dry weight (Sdw; g), root dry weight (Rdw; g), shoot:root dry weight ratio (S:R), final SCN population densities† (Pf), and reproductive factors‡ (Rf) for six levels of initial SCN population density (Pi) in an eight week growth chamber experiment.

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
BSR101	0	10	293	4.2	2.4	1.8	0	—
	100	9	202	1.4	2.0	0.7	63 522	635
	500	9	184	0.9	1.7	0.5	49 467	99
	1000	8	161	0.6	1.4	0.4	46 211	46
	2000	8	140	0.5	0.8	0.4	34 444	17
	4000	8	139	0.3	0.8	0.8	46 733	12
	LSD(0.05)	1	39	0.4	0.5	0.2	26 444	165
CX366	0	10	549	4.0	3.0	1.5	0	—
	100	10	328	1.8	2.9	0.7	44 560	445
	500	9	248	0.6	1.8	0.5	32 711	65
	1000	9	233	0.8	1.6	0.4	35 389	35
	2000	8	209	0.3	0.8	0.4	31 000	16
	4000	7	152	0.2	0.5	0.3	33 000	8
	LSD(0.05)	1	108	0.5	1.1	0.2	25 087	143
Jack	0	12	301	3.6	2.4	1.5	0	—
	100	11	279	2.9	2.1	1.4	1 222	12
	500	11	267	3.2	2.5	1.3	4 411	9
	1000	11	248	3.0	2.5	1.2	5 611	6
	2000	11	229	2.3	2.2	1.1	9 122	5
	4000	10	232	2.0	2.0	1.0	12 022	3
	LSD(0.05)	1	44	0.6	NS§	0.2	3798	6

Table 30. (continued).

Genotype	Pi	Node	Hgt	Sdw	Rdw	S:R	Pf	Rf
Probst	0	11	435	3.9	2.4	1.7	0	—
	100	11	331	1.4	2.4	0.6	46 789	468
	500	10	267	1.0	1.9	0.6	44 589	89
	1000	10	227	0.6	1.6	0.4	40 733	41
	2000	10	201	0.4	0.8	0.4	54 756	27
	4000	7	153	0.3	0.7	0.4	35 733	9
	LSD(0.05)	1	77	0.3	0.4	0.2	19 569	108
S24-92	0	10	442	3.9	2.4	1.8	0	—
	100	10	334	2.2	2.3	1.0	64 622	646
	500	10	237	0.9	1.9	0.5	39 822	80
	1000	9	234	0.7	1.5	0.4	24 844	25
	2000	9	186	0.4	0.8	0.5	27 411	14
	4000	7	152	0.3	0.6	0.6	46 778	12
	LSD(0.05)	1	56	0.5	0.5	0.3	21 978	166
Sturdy	0	10	331	3.6	2.6	1.5	0	—
	100	10	292	2.0	2.7	0.8	56 189	562
	500	9	203	0.8	1.8	0.5	40 711	81
	1000	9	212	0.8	1.6	0.4	57 711	58
	2000	8	169	0.5	1.1	0.4	53 233	27
	4000	6	135	0.3	0.7	0.4	47 300	12
	LSD(0.05)	1	41	0.6	0.5	0.2	26 064	187

Values presented are means of nine replications.
† SCN population densities expressed as eggs 100^{-1} cm^{-3} potting mix.
‡ Rf = Pf÷Pi.
§ NS = not significant.

Table 31. Results of linear regression analysis of plant height (Height) and shoot dry weight versus initial SCN population density (eggs 100^{-1} cm^{-3} potting mix) in an eight week growth chamber experiment.

	Height (mm)				Shoot dry weight (g)			
Genotype	Slope	Y intercept	R^2	Rank	Slope	Y intercept	R^2	Rank
BSR101	-0.0265 **	220.2	0.28	2	-0.00052 **	1.96	0.25	2
CX366	-0.0654 **	369.5	0.27	6	-0.00062 **	2.07	0.35	6
Jack	-0.0150 **	278.5	0.16	1	-0.00034 **	3.28	0.24	1
Probst	-0.0547 **	338.4	0.30	4	-0.00054 **	1.93	0.34	3
S24-92	-0.0549 **	331.9	0.38	5	-0.00062 **	2.17	0.38	5
Sturdy	-0.0411 **	275.9	0.46	3	-0.00057 **	2.06	0.37	4
LSD(0.05)	0.0103				0.00063			

** significant at the 0.01 probability level.

Table 32. Tolerance indices† (TI) of soybean genotypes for plant height and shoot dry weight in an eight week growth chamber experiment at five initial SCN population densities (Pi).

	Plant height						
	Pi (eggs 100^{-1} cm^{-3} soil)						
Genotype	100	500	1000	2000	4000	Mean	LSD(0.05)
BSR101	72	66	57	50	52	59	9
CX366	67	50	49	42	32	48	15
Jack	95	91	84	79	79	86	14
Probst	82	71	58	53	44	62	13
S24-92	77	55	54	44	38	54	8
Sturdy	93	66	66	55	43	65	10
LSD(0.05)	20	16	15	16	16	8	

	Shoot dry weight						
	Pi (eggs 100^{-1} cm^{-3} soil)						
Genotype	100	500	1000	2000	4000	Mean	LSD(0.05)
BSR101	32	21	12	6	14	17	9
CX366	49	15	19	8	4	19	14
Jack	84	91	86	67	55	77	18
Probst	35	25	16	10	8	19	7
S24-92	60	24	17	11	8	24	13
Sturdy	54	25	20	15	8	24	14
LSD(0.05)	25	16	12	12	9	9	

Values presented are means of nine replications.

† TI = (plant growth parameter in SCN-infested potting mix÷plant growth parameter in noninfested potting mix)×100.

HETERODERA GLYCINES INFECTION INCREASES INCIDENCE AND SEVERITY OF BROWN STEM ROT OF SOYBEAN[1]

A paper to be submitted to the Journal of Nematology

J. E. Behm and G. L. Tylka[2]

ABSTRACT

Interactions between *Heterodera glycines* and *Phialophora gregata*, the causal agent of brown stem rot (BSR) of soybean, were investigated in greenhouse and growth chamber experiments with soybean genotypes possessing various combinations of resistance or susceptibility to both pathogens. Overall average incidence and severity of

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stem discoloration characteristic of *P. gregata* infection was 259% and 732% greater, respectively, for all *H. glycines*-susceptible soybean genotypes when grown for eight weeks in the presence of both pathogens than when exposed to *P. gregata* alone. Increases in stem discoloration incidence and severity did not occur for PI 88.788-derived *H. glycines*-resistant genotypes. The increased incidence and severity of stem discoloration associated with *H. glycines* infection was detected in soybeans with Rbs1Rbs3, Rbs2, and Rbs3 genotypes for *P. gregata* resistance. In split-root plants, incidence of stem discoloration was 131% greater when *H. glycines* and *P. gregata* were inoculated on the same half-root system than when half-roots were inoculated with *P. gregata* alone. Additionally, incidence of stem discoloration was 57% greater when *H. glycines* and *P. gregata* were inoculated on separate half-roots than when plants were inoculated with *P. gregata* alone, although the difference was not significant at $P = 0.05$. No effect of *P. gregata* on total *H. glycines* reproduction was detected in any experiment. Results support field observations of increased symptoms of *P. gregata* infection of soybean when the nematode also is present.

INTRODUCTION

The soybean cyst nematode (*Heterodera glycines* Ichinohe) is estimated to be the most damaging pathogen of soybean in the north central United States, causing soybean production losses of 1.3×10^6 metric tons (Mg) per year, whereas losses of 5.3×10^5 Mg per year have been attributed to *Phialophora gregata* (Allington & Chamberlain)

Gams, the causal agent of brown stem rot (BSR) of soybean (Doupnik, 1993). Both pathogens are widely distributed throughout the Midwest (Tachibana and Booth, 1979; Workneh et al., 1996), and it is likely that soybeans growing in this region may be infected by both pathogens simultaneously. Several sources of soybean resistance to each pathogen have been identified, and both pathogens are managed by a combination of rotation to nonhost crops and growing resistant soybean cultivars.

Although interactions between plant-parasitic nematodes and other pathogen groups have been reported and reviewed (Powell, 1971; Powell, 1979), published research of interactions between *H. glycines* and other plant pathogens is limited (McGawley, 1992). Foliar symptoms of Fusarium wilt caused by *Fusarium oxysporum* Schlecht were greater for plants of 'Jackson' soybean grown in greenhouse soil infested with *F. oxysporum* and *H. glycines* than in soil infested with *F. oxysporum* alone (Ross, 1965). Similarly, severity of *Phytophthora sojae* (Kaufmann & Gerdemann) infection of 'Corsoy' and 'Dyer' soybean was greater in *H. glycines*-infested versus *H. glycines*-free greenhouse soil (Adeniji et al., 1975). In field microplot experiments, greater numbers of *H. glycines* females were produced on *Fusarium*-infected than noninfected 'Lee' soybean (Ross, 1965). Conversely, fewer *H. glycines* females developed on *P. sojae*-infected than on *P. sojae*-free 'Corsoy' soybean grown in a greenhouse experiment (Adeniji et al., 1975). *Phytophthora sojae* resistance of 'Harosoy 63' soybean in a greenhouse experiment was not affected by *H. glycines* infection, nor was *H. glycines* resistance in 'Dyer' soybean affected by *P. sojae* infection (Adeniji et al., 1975).

More recent research on interactions of *H. glycines* with fungal pathogens

involves *Fusarium solani* (Mart.) Sacc. f. sp. *glycines* form. nov. (Roy, 1997), the causal agent of soybean sudden death syndrome (SDS). Hershman et al. (1990) and Rupe et al. (1991) detected greater severity of SDS foliar symptoms for *H. glycines*-susceptible soybean cultivars than for *H. glycines*-resistant cultivars when grown in fields infested with both pathogens. *Heterodera glycines*-susceptible 'Coker 156' soybean had greater SDS incidence and severity in field microplots infested with both *H. glycines* and *F. solani* than when grown in microplots infested with *F. solani* alone (McLean and Lawrence, 1993a). Additionally, fewer *H. glycines* eggs were produced on *F. solani*-infected than on *F. solani*-free 'Coker 156' soybean.

Preliminary data and field observations (Behm and Tylka, unpub.; Tachibana, unpub.; Tubajika, Tylka, and Yang, unpub.) suggest increases in incidence and severity of *P. gregata* infection of soybean when grown in *H. glycines*-infested soil. Negishi and Kobayashi (1984) reported that *H. glycines* infection increased incidence of brown stem rot of adzuki bean, *Vigna angularis* (Willd.), in greenhouse experiments. However, there is no published research investigating interactions between *H. glycines* and *P. gregata*. The objective of this research was to determine the effects of *H. glycines* and *P. gregata* on each other and on growth and development of soybean in greenhouse and growth chamber environments.

MATERIALS AND METHODS

Soybean genotypes: The soybean genotypes included in the described experiments possess various combinations of resistance or susceptibility to both *H. glycines* and *P. gregata*. 'Sturdy' and 'Harosoy' are susceptible to both pathogens (Orf et al., 1991; Weiss and Stevenson, 1955). 'BSR101' is *H. glycines*-susceptible and has *P. gregata* resistance derived from the plant introduction PI 84.946-2 which, apparently, contains the Rbs1 and Rbs3 genes for *P. gregata* resistance (Eathington et al., 1995). 'BSR101' possesses the Rbs3 and, possibly, the Rbs1 gene (Eathington et al., 1995). 'Bell', 'Freeborn', and 'Jack' possess PI 88.788-derived *H. glycines* resistance and are susceptible to *P. gregata* (J. H. Orf, pers. comm.; Nickell et al., 1990a, 1990b). 'Newton' has 'Peking'-derived *H. glycines* resistance and is *P. gregata* susceptible (Mansur et al., 1991). 'PS2465N' also has 'Peking'-derived *H. glycines* resistance and is *P. gregata* resistant (source unknown). 'IA1006' and 'IA2008R' have *P. gregata* resistance originally derived from 'BSR101' and are *H. glycines* susceptible (S. P. Schultz, pers. comm.). L67-6301 and L68-0107 are 'Harosoy' isolines with *P. gregata* resistance (BSR resistance genes unknown) derived from backcrosses to PI 84.946-2 (C. D. Nickell, pers. comm.) and are *H. glycines* susceptible. LN92-12033 and LN92-12054 are near-isogeneic lines developed at the University of Illinois (C. D. Nickell, pers. comm.). LN92-12033 contains the Rbs2 gene for *P. gregata* resistance from PI 437.833, whereas LN92-12054 is *P. gregata* susceptible (rbs2); both LN92-12033 and LN92-12054 are *H. glycines* susceptible.

Heterodera glycines inoculum: *H. glycines* race 3 egg inoculum was produced on *H. glycines*-susceptible 'Corsoy 79' soybean in greenhouse pots. Eggs were obtained by dislodging females from roots of infected plants with a stream of water, plus wet-sieving and decanting (Gerdemann, 1955) of *H. glycines*-infested soil. Females and cysts were recovered on a 250-μm-pore sieve nested below an 850-μm-pore sieve. Eggs were released from females and cysts by crushing suspensions of the nematodes in water with a motorized pestle (Niblack et al., 1993), and eggs were collected on a 25-μm-pore sieve nested under a 75-μm-pore sieve. Eggs were separated from plant debris and soil particles by centrifugal flotation (Niblack et al., 1993) and counted by direct microscopic observation.

Effect of H. glycines on soybean BSR symptom development: Two-week-old cultures of *P. gregata* isolated from 'Kenwood' soybean grown at the Iowa State University Curtiss Research Farm (F. Workneh, pers. comm.) and grown on soybean stem agar (Allington and Chamberlain, 1948) were cut into approximately 1-cm^2 sections, and the agar cubes containing *P. gregata* were transferred to flasks containing 60 ml of sterile soybean stem broth. The broth was made from 25 g of greenhouse-grown soybean stems blended in approximately 300 ml deionized water, strained through gauze cloth, and diluted to one L with deionized water. The fungal cultures were incubated on a rotary shaker for 12 days at room temperature (approximately 22°C). The conidia produced were counted, and approximately 2.4×10^8 *P. gregata* conidia in 600 ml of water were sprayed onto each of two 1,200 g lots of twice-autoclaved (one hour at a pressure of 1.4

kg per cm^2 and 126°C in autoclavable bags), field-grown soybean straw collected after harvest. *Phialophora gregata* population densities (conidia per g straw) were determined after 15 days of incubation at room temperature by agitating a weighed subsample of straw inoculum in deionized water and counting conidia by direct microscopic observation. One lot of infested straw was re-autoclaved for use as a control in *P. gregata*-free treatments, and *H. glycines* eggs were autoclaved for use as a control in *H. glycines*-free treatments to ensure uniform physical properties of the potting mixes used in each pathogen treatment.

Pathogen inocula were thoroughly mixed into an autoclaved, 1:1 sand-soil potting mix, and the infested mix was placed in 15-cm-diam., 1.75-L-capacity clay pots. Pathogen treatments were as follows: control (1,200 autoclaved *H. glycines* eggs plus two g autoclaved straw per 100 cm^3 potting mix), *H.g.* (1,200 *H. glycines* eggs plus two g autoclaved straw per 100 cm^3 potting mix), *P.g.* (1,200 autoclaved *H. glycines* eggs plus two g straw containing approximately 1.5×10^8 *P. gregata* conidia per 100 cm^3 potting mix), and *H.g.+P.g.* (1,200 *H. glycines* eggs plus two g straw containing approximately 1.5×10^8 *P. gregata* conidia per 100 cm^3 potting mix).

Five seeds of 'Sturdy', 'BSR101', 'Bell', 'Freeborn', 'Newton', or 'PS2465N' soybean were planted in each pot. The pots were arranged in a Conviron (Controlled Environments, Pembina, ND) model CMP3023 growth chamber in a randomized complete block design with four replications per pathogen treatment, and plants were thinned to two plants per pot after emergence. A temperature of 22°C ± 1 C° and a 16 hour photoperiod were maintained throughout the experiment. Nine weeks after

planting, the soybean plants were severed at the soil surface, and shoot height and fresh weight were determined for each plant. The stems of each plant were split longitudinally, and the length from the soil-line of internal stem discoloration characteristic of *P. gregata* infection was measured. Incidence (presence or absence) and severity [(height of stem discoloration÷total plant height)×100] of stem discoloration characteristic of *P. gregata* infection were calculated for each plant. Final *H. glycines* soil egg population densities (Pf) were determined for each pot by extracting *H. glycines* females and cysts from 100 cm^3 aliquants of potting mix by elutriation (Byrd et al., 1976). *Heterodera glycines* eggs were extracted from cysts and females as described above.

One 0.5-cm-long stem section from each of 12 arbitrarily selected plants exhibiting pith discoloration characteristic of *P. gregata* infection from the *P. gregata*-infested treatments and 12 arbitrarily selected asymptomatic plants from treatments without *P. gregata* were surface disinfested in 0.25% NaOCl for two minutes, rinsed for a minimum of two minutes in sterile, deionized water, and plated on selective media (Mengistu et al., 1991) for isolation of *P. gregata*. *Phialophora gregata* was identified by colony growth rate and morphology after incubation at 20°C for two weeks (Mengistu and Grau, 1986).

Data for plant growth, incidence and severity of stem discoloration, and Pf were subjected to analysis of variance (ANOVA), and Fisher's least significant difference (LSD) test ($P = 0.05$) was used to separate treatment means when significant differences were detected (Cochran and Cox, 1992).

The experiment was repeated in a Conviron model CMP3244 growth chamber with 1.5 g of straw inoculum containing approximately 1.7×10^8 *P. gregata* conidia per 100 cm^3 potting mix used as *P. gregata* inoculum. *Heterodera glycines* inoculum was the same as for the first trial of the experiment.

Comparison of soybean genotypes containing the 'BSR101' source of BSR resistance: An experiment was conducted to determine whether *H. glycines* infection affected BSR symptom development in several 'BSR101'-derived BSR-resistant soybean genotypes. *Phialophora gregata*-infested soybean straw was collected from fields after the 1996 harvest for use as *P. gregata* inoculum because production of sufficient quantities of the artificially infested straw inoculum proved to be unreliable. The straw was stored at 5°C and ground through a 0.5-mm-diam. screen as needed for use as *P. gregata* inoculum. Population densities of approximately 1×10^4 *P. gregata* colony forming units (cfu) per g infested straw were determined by serial dilution. Soybean straw for the control and *H.g.* treatments was autoclaved (one hour at a pressure of 1.4 kg per cm^2 and 126°C) twice. The pathogen treatments were: control (three g autoclaved straw per 100 cm^3 potting mix); *H.g.* (1,200 *H. glycines* eggs plus three g autoclaved straw per 100 cm^3 potting mix); *P.g.* (30,000 *P. gregata* cfu in three g straw per 100 cm^3 potting mix); and *P.g.+H.g.* (1,200 *H. glycines* eggs plus 30,000 *P. gregata* cfu in three g straw per 100 cm^3 potting mix). Pathogen inoculum was mixed into a sand-soil potting mix as described above. The control and *P.g.* treatments did not receive autoclaved *H. glycines* eggs to avoid recovery of the autoclaved eggs from the potting

mix at completion of the experiment.

Five seeds of 'BSR101', 'Sturdy', 'Freeborn', 'Jack', 'IA1006', or 'IA2008R' soybean were planted in the same experimental design as described above. Temperature and light were maintained as previously described, and shoot height and fresh weight, incidence and severity of stem discoloration characteristic of *P. gregata* infection, and Pf were determined after eight weeks.

Culture of stem sections from arbitrarily selected plants on a selective medium for verification of *P. gregata* infection was as described above. The experiment was conducted once in each of the two described growth chambers, and the data were subjected to analysis as described above.

Comparison of soybean genotypes with different BSR resistance genes: To determine whether *H. glycines* infection affected BSR symptom development in genotypes containing different genes for BSR resistance, five seeds of the soybean genotypes 'BSR101', 'Sturdy', 'Harosoy', L67-6301, L68-0107, LN92-12033, and LN92-12054 were planted in the same experimental design and pathogen treatment combinations as described for the experiment comparing 'BSR101'-derived BSR-resistant genotypes, except that the control and *H.g.* treatments did not include autoclaved soybean straw. Temperature within the growth chamber was reduced to 20°C seven weeks after planting to enhance development of stem discoloration (Schneider et al., 1972). Shoot height and fresh weight, incidence and severity of stem discoloration characteristic of *P. gregata* infection, and Pf were determined after eight weeks, and the data were

subjected to analysis as described above.

Split-root experiment: To determine whether the effect of *H. glycines* on BSR symptom development was a localized or systemic phenomenon, split-root experiments were conducted. The lower one-half of the tap roots of one-week-old 'BSR101' seedlings germinated in vermiculite were excised, and approximately three cm of the remainder of the tap roots were split lengthwise with a razor blade. A 2-cm-long portion of plastic pot label was placed between the two root halves of each seedling to ensure development of a split root system, and the seedlings were transplanted into an autoclaved, 1:1 sand-soil potting mix. Eight days after the roots were split, the plants were removed from the potting mix, and individual plants with uniform development of both half-root systems were selected and transplanted into 10-cm^2 plastic pots, which were stapled together in pairs to form double-pot units. Each half-root system of each plant was trained into a separate single pot of a double-pot unit. The single pots of each double-pot unit contained a 1:1 sand-soil potting mix infested with *H. glycines* (1,200 eggs per 100 cm^3 potting mix) and *P. gregata* (30,000 cfu in three g soybean straw per 100 cm^3 potting mix) in various combinations together and separately. Single pots designated as "—" or *H.g.* contained potting mix with three g of twice-autoclaved (one hour at a pressure of 1.4 kg per cm^2 and 126°C), *P. gregata*-infested soybean straw per 100 cm^3 as a control. The double-pot units were arranged on a greenhouse bench in a randomized complete block design. A temperature of 22°C $\pm$ 2 C° was maintained, and the photoperiod was extended to 16 hours by supplemental lighting.

Shoot height and fresh weight and extent of stem discoloration characteristic of *P. gregata* infection were determined for each plant eight weeks after transplanting into the double pot units. Half-root systems were removed from each single pot, were soaked in water to remove adhering potting mix, and were blotted dry and weighed. Additionally, *H. glycines* Pf for each single pot was determined by methods described above. The split-root experiment was conducted three times utilizing autoclaved, sand-soil potting mix and once with a nonsterile potting mix. The data were subjected to analysis as described above.

RESULTS

Similar results were obtained among the trials within each experiment, therefore, data for each experiment were combined for analysis. Significant differences among means were determined at $P \leq 0.05$.

Effect of H. glycines on soybean BSR symptom development: Data were originally analyzed with a two-factor ANOVA model. Significant genotype by pathogen treatment interactions were detected for each response variable; data subsequently were sorted by genotype and pathogen treatment and analyzed. The effect of the pathogen treatments on shoot height varied among genotypes (Table 1). Shoot height of 'BSR101' and 'Sturdy' was less ($P \leq 0.05$) in all pathogen-inoculated treatments than in the control treatment. However, no differences in height among pathogen treatments were detected

for 'Bell', 'Newton', or 'PS2465N'. Height of 'Freeborn' in the control treatment (242 mm) was not different than height in the *H.g.* or *H.g.+P.g.* treatments, but was greater ($P \leq 0.05$) than height in the *P.g.* treatment (214 mm). 'Bell' was the tallest of all cultivars in the control treatment (373 mm), whereas 'Newton' was the tallest in the *H.g.*, *P.g.*, and *H.g.+P.g.* treatments. 'Freeborn' was the shortest cultivar in the control treatment (242 mm). Differences ($P \leq 0.05$) in height among cultivars were detected for each pathogen treatment, however, trends for height among cultivars were not consistent among the pathogen treatments.

In most cases, pathogen treatments infested with *H. glycines* had significantly less shoot weights than treatments not infested with the nematode (Table 2). Shoot weight of 'Sturdy' was less ($P \leq 0.05$) in the *H.g.* and *H.g.+P.g.* treatments (4.1 and 3.7 g, respectively) than in the control and *P.g.* treatments (10.8 and 8.1 g, respectively), and shoot weight of 'Sturdy' in the *P.g.* treatment (8.1 g) was less ($P \leq 0.05$) than that in the control treatment (10.8 g). Similarly, shoot weight of 'BSR101' in the *H.g.* and *H.g.+P.g.* treatments (3.8 and 2.8 g, respectively) was less ($P \leq 0.05$) than that in the control and *P.g.* treatments (10.0 and 9.1 g, respectively). No differences in weight of 'Bell' or 'PS2465N' were detected among pathogen treatments. Shoot weight of 'Freeborn' in the *P.g.* treatment (8.5 g) was not different than shoot weight in the *H.g.+P.g.* treatment (9.1 g), but was less ($P \leq 0.05$) than shoot weight in the control and *H.g.* treatments (10.4 and 10.3 g, respectively). Differences in shoot weight among cultivars were detected for each pathogen treatment. 'Newton' had the greatest shoot weight among cultivars in the control and *H.g.* treatments, whereas 'Bell'

had the greatest shoot weight among cultivars in the *P.g.* and *H.g.+P.g.* treatments.

Incidence of stem discoloration was greater in the *H.g.+P.g.* treatment than in the *P.g.* treatment for all genotypes, but differences between these treatments were significant only for 'Sturdy', 'BSR101', and 'Newton' (Table 3). Incidence of stem discoloration of 'Sturdy' in the *P.g.* treatment (50%) was greater ($P \leq 0.05$) than that of any other cultivar. Incidence of stem discoloration of 'Sturdy', 'BSR101', and 'Newton' in the *H.g.+P.g.* treatment was greater ($P \leq 0.05$) than that of 'Bell', 'Freeborn', and 'PS2465N'. One 'Sturdy' plant in the *H.g.* treatment had a slight amount of stem discoloration characteristic of *P. gregata* infection. Attempts to isolate *P. gregata* from plants in the control and *H.g.* treatments were not successful; however, *P. gregata* was isolated from stems of all of the tested plants grown in potting mix infested with *P. gregata.*

In addition to increasing the incidence of stem discoloration, *H. glycines* increased the severity of the discoloration in pathogen treatments containing both pathogens (Table 4). Severity of stem discoloration of 'Sturdy', 'BSR101', and 'Newton' in the *H.g.+P.g.* treatment was greater ($P \leq 0.05$) than that of 'Bell', 'Freeborn', and 'PS2465N'. No differences in severity of stem discoloration among 'Sturdy', 'BSR101', and 'Newton' (43, 43, and 49%, respectively) or among 'Bell', 'Freeborn', and 'PS2465N' (3, 3, and 2%, respectively) were detected in the *H.g.+P.g.* treatment. Additionally, severity of stem discoloration of 'Sturdy', 'BSR101', and 'Newton' was greater in the *H.g.+P.g.* treatment than in the *P.g.* treatment. No differences in severity of stem discoloration among cultivars were

detected in the control, *H.g.*, and *P.g.* treatments.

Heterodera glycines population densities increased on all *H. glycines*-susceptible but not on all *H. glycines*-resistant cultivars (Table 5). Differences in Pf among cultivars were detected for the *H.g.* and *H.g.+P.g.* treatments. The *H. glycines*-susceptible cultivars had greater Pf than the *H. glycines*-resistant cultivars, but no differences in Pf among the *H. glycines*-susceptible or among the *H.glycines*-resistant cultivars were detected. Final *H. glycines* population densities in the *H.g.* treatment ranged from 775 eggs per 100 cm^3 potting mix for 'Newton' to 89,288 eggs per 100 cm^3 potting mix for 'Sturdy' and from 539 eggs per 100 cm^3 potting mix for 'Newton' to 113,825 eggs per 100 cm^3 potting mix for 'Sturdy' in the *H.g.+P.g.* treatment. Also, differences in Pf between the *H.g.* and *H.g.+P.g.* treatments were not significant for any cultivar when the control and *P.g.* treatments were not included in the data analysis.

Comparison of soybean genotypes containing the 'BSR101' source of BSR resistance: Data were originally analyzed with a two-factor ANOVA model. Significant genotype by pathogen treatment interactions were detected for all response variables except height. Consequently, data were sorted by genotype and pathogen treatment and analyzed. Generally, shoot heights were less in the *H. glycines*-infested treatments than in treatments without the nematode (Table 6). Plants of 'BSR101', 'Freeborn', 'IA2008R', and 'Sturdy' were shorter ($P \leq 0.05$) in the *H.g.* and *H.g.+P.g.* treatments than in the control and *P.g.* treatments, but no differences in height were detected

between the *H.g.* and *H.g.+P.g.* treatments or between the control and *P.g.* treatments. No differences in height among pathogen treatments were detected for 'Jack' or 'IA1006'. 'Jack' was the shortest genotype in each pathogen treatment, and 'IA2008R' was the tallest in each pathogen treatment, except *H.g.* Differences ($P \leq 0.05$) in height among genotypes were detected in the control, *H.g.*, and *P.g.* treatments, but not in the *H.g.+P.g.* treatment.

Differences in shoot fresh weight among the pathogen treatments were detected for all cultivars (Table 7). Shoot weights of 'BSR101' and 'Sturdy' were less ($P \leq 0.05$) in the *H.g.* and *H.g.+P.g.* treatments than in the control and *P.g.* treatments, but there were no differences in shoot weight of these genotypes between the *H.g.* and *H.g.+P.g.* treatments or between the control and *P.g.* treatments. Shoot weights of all of the remaining genotypes, except 'Jack', were less ($P \leq 0.05$) in the *H.g.* treatment than in all other pathogen treatments.

Incidence of stem discoloration characteristic of *P. gregata* infection was affected similarly by *H. glycines* in all of the *P. gregata*-resistant soybean genotypes (Table 8). Greater incidence of stem discoloration was detected for all genotypes in the *H.g.+P.g.* treatment than in the *P.g.* treatment. However, the difference between the two pathogen treatments was not significant for 'Jack' when data from the control and *H.g.* treatments were not included in the analysis. No differences in incidence of stem discoloration among 'BSR101', 'IA1006', 'IA2008R', and 'Sturdy' were detected in the *H.g.+P.g.* treatment. 'Freeborn' and 'Jack' had less ($P \leq 0.05$) incidence of stem discoloration (44 and 38%, respectively) in the *H.g.+P.g.* treatment than did all of the

H. glycines-susceptible genotypes, except 'IA1006' (69%). Stem discoloration was observed in several plants of 'Sturdy' and 'BSR101' in the control and *H.g.* treatments, but attempts to isolate the pathogen from these stems were not successful. In contrast, *P. gregata* was isolated from the stem of each arbitrarily selected plant grown in potting mix infested with *P. gregata.*

Severity of stem discoloration differed among genotypes for all pathogen treatments and among pathogen treatments for most genotypes (Table 9). Stem discoloration severity was greater ($P \leq 0.05$) in the *H.g.+P.g.* treatment than in the *P.g.* treatment for all genotypes, except 'Jack'. Severity of stem discoloration of 'Sturdy' in the *H.g.+P.g.* treatment (49%) was greater ($P \leq 0.05$) than that for all other genotypes in the experiment.

Final *H. glycines* egg population densities were greater for all *H. glycines*-susceptible genotypes than for *H. glycines*-resistant genotypes in both *H. glycines*-infested treatments (Table 10). Final *H. glycines* population densities in the *H.g.* treatment ranged from 300 eggs per 100 cm^3 potting mix for 'Jack' to 8,025 eggs per 100 cm^3 potting mix for 'Sturdy'. 'Freeborn' had the least Pf (100 eggs per 100 cm^3 potting mix) and 'Sturdy' had the greatest Pf (12,338 eggs per 100 cm^3 potting mix) in the *H.g.+P.g.* treatment. Final nematode densities for all *H. glycines*-susceptible genotypes were greater ($P \leq 0.05$) than that for *H. glycines*-resistant genotypes in the *H.g.* and *H.g.+P.g.* treatments; no differences in Pf among the *H.g.*-susceptible genotypes or between the *H. glycines*-resistant genotypes were detected. 'BSR101' and 'IA2008R' had greater Pf in the *H.g.+P.g.* treatment than in the *H.g.* treatment and

'Freeborn' had less Pf in the *H.g.+P.g.* treatment than in the *H.g.* treatment. However, differences in Pf between the *H.g.* and *H.g.+P.g.* treatments were not significant for any genotype when the control and *P.g.* treatments were not included in the data analysis.

Comparison of soybean genotypes with different BSR resistance genes: Shoot heights of the genotypes were significantly less in the pathogen treatment containing both pathogens than in the other pathogen treatments (Table 11). Differences in shoot height among genotypes were detected in all pathogen treatments except *P.g.*, and differences in height among pathogen treatments were significant for all genotypes. 'Harosoy' was shorter ($P \leq 0.05$) in the *P.g.* treatment (241 mm) than in the *H.g.* treatment (265 mm), but no differences in height between the *H.g.* and *P.g.* treatments were detected for any other genotype. LN92-12033 was the tallest genotype in each pathogen treatment.

Shoot weights of each genotype were significantly less in the treatment containing both pathogens than in the treatment containing *P. gregata* alone (Table 12). Differences in shoot fresh weight among pathogen treatments were detected for all genotypes, but differences in shoot weight among genotypes were significant only in the *H.g.+P.g.* treatment. Shoot weight of each genotype was less ($P \leq 0.05$) in the *H.g.+P.g.* treatment than in the other pathogen treatments. Additionally, shoot weight in the *P.g.* treatment was less ($P \leq 0.05$) than that in the control and *H.g.* treatments for all genotypes, except L67-6301.

Significantly greater incidence of stem discoloration characteristic of *P. gregata*

infection was detected in the treatments containing both pathogens than in the treatment containing *P. gregata* alone (Table 13). Incidence of stem discoloration was greater ($P \leq 0.05$) in the *H.g.*+*P.g.* treatment than in the *P.g.* treatment for all genotypes, except 'Sturdy'. 'Sturdy' had a greater ($P \leq 0.05$) incidence of stem discoloration (100%) in the *P.g.* treatment than any other genotype. Differences in incidence among the remainder of the genotypes in the *P.g.* treatment were not significant. Incidence of stem discoloration in the *H.g.*+*P.g.* treatment was greater ($P \leq 0.05$) than that in the *P.g.* treatment for all genotypes, except 'Sturdy' (100% in both pathogen treatments), however, the differences in incidence for L67-0107 and LN92-12033 were not significant when the control and *H.g.* treatments were not included in the data analysis. No differences in incidence of stem discoloration among genotypes were detected in the *H.g.*+*P.g.* treatment.

Plants of each genotype grown in potting mix infested with both pathogens had greater severity of stem discoloration than plants grown in mix infested with *P. gregata* alone (Table 14). Severity of stem discoloration of 'Sturdy' (100%) in the *H.g.*+*P.g.* treatment was greater ($P \leq 0.05$) than that for all other genotypes. Severity of stem discoloration was greater in the *H.g.*+*P.g.* than in the *P.g.* treatment for each genotype, however, the difference between the two pathogen treatments was not significant for LN92-12033 when the control and *H.g.* treatments were not used in the data analysis.

Few significant differences in Pf were detected between the pathogen treatment containing both pathogens and the *H. glycines* only treatment (Table 15). Final

nematode densities were greater for L67-6301 and L68-0107 in the *H.g.+P.g.* treatment than in the *H.g.* treatment. There were no differences in *H. glycines* Pf among genotypes in the *H.g.+P.g.* or *H.g.* treatments. Additionally, Pf in the *H.g.+P.g.* and *H.g.* treatments were not significantly different for any genotype when the control and *P.g.* treatments were not included in the data analysis.

Split-root experiment: The different pathogen treatment combinations affected shoot height, but not half-root or shoot weights (Table 16). No differences in half-root weight between the single pots of each pathogen treatment were detected. Half-root weights in the *H.g.*|*P.g.* treatment were numerically less than half-root weights in all other treatments, and although the differences were not significant at $P = 0.05$ they were significant at $P = 0.10$ (data not shown). Plants in the *H.g.*|—, *H.g.*|*P.g.*, and *H.g.+P.g.*|— treatments (426, 411, and 456 mm, respectively) were shorter ($P \leq 0.05$) than those in the —|— and *P.g.*|— treatments (556 and 557 mm, respectively). No differences in shoot weight among pathogen treatments were detected.

Incidence and severity of stem discoloration were both affected by the pathogen treatment combinations. Differences ($P \leq 0.05$) in incidence of stem discoloration characteristic of *P. gregata* infection among pathogen treatments were detected. Incidence of stem discoloration in the *H.g.*|*P.g.* treatment (46%) was intermediate to, but not different from, that in either the *H.g.+P.g.*|— (67%) or *P.g.*|— (29%) treatments, although incidence of stem discoloration in the *H.g.*|*P.g.* treatment was greater than that in the *P.g.*|— treatment. Severity of stem discoloration in the

H.g.+P.g.|— treatment (18%) was greater ($P \leq 0.05$) than that in the *H.g.*|*P.g.* (10%) and *P.g.*|— (6%) treatments.

No differences in number of *H. glycines* females, total eggs per half-root, soil egg Pf, and total egg Pf were detected among the *H. glycines*-infested treatments. Eggs per female in the *H.g.*|— treatment (199) was intermediate to but not different from that in the *H.g.*|*P.g.* and *H.g.+P.g.*|— treatments (224 and 149, respectively) although eggs per female was less in the *H.g.+P.g.*|— treatment than in the *H.g.*|*P.g.* treatment. Final egg population densities were similar to Pi for all single pots infested with *H. glycines*.

DISCUSSION

Results of our research substantiate field observations of increased symptoms of BSR of soybean when plants also are infected with *H. glycines*. In our studies, incidence and severity of soybean stem discoloration characteristic of *P. gregata* infection was greater in potting mix infested with both pathogens than in potting mix infested with *P. gregata* alone. The increased incidence and severity of stem discoloration occurred for all *H. glycines*-susceptible soybean genotypes, regardless of *P. gregata* resistance genes present in the individual genotypes. A similar increase in incidence of stem discoloration was detected in a 'Peking'-derived *H. glycines*-resistant, *P. gregata*-susceptible cultivar, but not in PI 88.788-derived *H. glycines*-resistant cultivars. These results support previous observations of an association between PI

88.788-derived *H. glycines* resistance and resistance to *P. gregata* (MacGuidwin et al., 1995).

Although *P. gregata* infection of soybean may occur early in the growing season, BSR symptoms typically are not expressed until later stages of soybean development. Our research was conducted in a much shorter time frame than that which occurs in a soybean growing season. Therefore, field evaluations are needed to reveal how *H. glycines* and *P. gregata* interact in a field environment and to determine the effect the interaction between the two pathogens has on soybean yield. Niblack et al. (1992) observed that stem browning of 'BSR101' in an *H. glycines*-infested field in Iowa was comparable to that of the *P. gregata*-susceptible soybean cultivar 'Elgin' at the end of the growing season in 1986 and 1987, but similar stem discoloration was not observed with the *P. gregata*-resistant soybean cultivar 'BSR201'. It was not reported whether *P. gregata* was isolated from the discolored 'BSR101' stems in their experiments, nor is it known whether the presence of the fungus was confirmed throughout all plots of the study area.

The influence of *H. glycines* on stem discoloration in our studies was detected in both sterile and non-sterile potting mixes and in potting mix containing straw naturally or artificially infested with *P. gregata*. Mengistu et al. (1991) recovered 6×10^4 to 1×10^6 *P. gregata* cfu per g of ground straw collected from a soybean field in the spring following a fall soybean harvest, whereas we recovered 1×10^4 cfu per g of the naturally-infested straw used in our experiments. In field microplots, Adee et al. (1995) detected low severity of BSR symptoms when *P. gregata* densities were less than $1 \times$

10^7 cfu per m^2. However, inoculum density expressed as cfu per 100 cm^3 potting mix in our experiments and cfu per m^2 in microplots are not comparable. Furthermore, we could not critically compare inoculum levels between the naturally-infested and artificially-infested straw inocula used in our experiments because of the different methods used to enumerate inoculum density dictated by the distinct physical properties of the two *P. gregata* sources.

Other soybean pathogens, including *Acremonium* sp., may cause stem discoloration similar to that of *P. gregata* infection (Mengistu and Grau, 1986). However, we are confident that we were observing stem discoloration symptoms characteristic of *P. gregata* infection because the *P. gregata* isolate used for the artificial inoculum experiments was verified as *P. gregata* prior to start of the experiment (Workneh, pers. comm.), and fungi that we isolated from naturally-infested straw and stem sections from the experiments were verified as *P. gregata* based on colony growth rate and morphology characteristics (Mengistu and Grau, 1986; Mengistu et al., 1991).

The effects of the different pathogen treatments on shoot height and fresh weight were not consistent among experiments and genotypes in our studies. However, measurements of these plant growth parameters were not crucial to our investigation. In the split-root experiment, half-root weight was suppressed when the two pathogens were inoculated on separate half-roots of the same plant, but not when only one half-root system was infected by either pathogen alone or both pathogens together. It is possible that the uninfected half-root system allowed the plant to produce compensatory

growth of the pathogen-infected half-roots.

Split-root experiments of McLean and Lawrence (1993b) revealed that leaf symptoms of *F. solani* infection of 'Coker 156' soybean were significantly greater when both pathogens were inoculated onto the same half-root system than when each pathogen was inoculated onto separate half-root systems or when half-root systems were inoculated with *F. solani* alone. They concluded that the influence of *H. glycines* on *F. solani* infection of soybean was not systemic. In our split-root studies, we observed an increase in incidence of stem discoloration when *H. glycines* and *P. gregata* were inoculated on separate half-root systems than when half-roots were inoculated with *P. gregata* alone. This increase was consistent among the six replications of each of the four experiments, but was not significant at $P = 0.05$. However, we believe it is likely that the effect of *H. glycines* on BSR stem discoloration is systemic.

We did not detect any effect of *P. gregata* on total nematode reproduction in any experiment, although inoculation of both pathogens on the same half-root system in our split-root experiment suppressed nematode fecundity. Carris et al. (1986) isolated *P. gregata* from *H. glycines* cysts extracted from field soil, but did not investigate whether the nematode was being parasitized by the fungus. Considering the decreased *H. glycines* fecundity associated with *P. gregata* in our split-root studies, suppression of final *H. glycines* soil population densities by *P. gregata* might have been observed in our studies if the experiments had continued for a longer period of time.

Our experiments did not attempt to elucidate specific mechanisms of the interaction between the two pathogens. The nematode causes physiological changes and

physical damage in the soybean root as it initiates syncytial development, which may affect resistance to or symptom expression of *P. gregata* infection. Other possible mechanisms of the effect of *H. glycines* on BSR symptom development are root system stress caused by nematode infection or creation of entry sites for *P. gregata* caused by activity of the nematode. The latter hypothesis probably does not involve entry wounds by *H. glycines* second-stage juveniles, though, because *H. glycines*-resistant and susceptible soybean genotypes are penetrated equally by the juveniles (Acedo et al., 1984) but we observed that PI 88.788-derived *H. glycines*-resistant soybean cultivars did not exhibit increased stem discoloration.

Our research suggests that a combination of resistance to both pathogens is desirable to minimize *P. gregata* infection of soybean when both pathogens are present although it is possible that infection of soybean by the *P. gregata* fungus may be less affected by *H. glycines* infection than is stem discoloration symptom development. *Heterodera glycines* population densities should be below detectable levels in soils utilized for field evaluation of soybean genotypes for *P. gregata* reaction because infection by the nematode is likely to alter genotype reaction to *P. gregata*. Finally, *H. glycines* resistance derived from PI 88.788 appears to be associated with resistance to *P. gregata* symptom development and might be useful in soybean breeding programs for resistance to both pathogens.

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Table 1. Height (mm) of soybean cultivars after nine weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with artificially infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Cultivar	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	S	289	216	230	190	35
BSR101	S	R	307	203	275	198	27
Bell	R (PI88)[c]	S	373	287	276	282	NS
Freeborn	R (PI88)	S	242	254	214	218	28
Newton	R (Pek)[d]	S	347	329	312	300	NS
PS2465N	R (Pek)	R	298	298	301	267	NS
LSD			52	31	33	27	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.
[d] R (Pek) = Peking-derived *H. glycines* resistance.

Table 2. Shoot fresh weight (g) of soybean cultivars after nine weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with artificially infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Cultivar	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	S	10.8	4.1	8.1	3.7	1.6
BSR101	S	R	10.0	3.8	9.1	2.8	1.3
Bell	R (PI88)[c]	S	10.7	10.3	9.6	9.9	NS
Freeborn	R (PI88)	S	10.4	10.3	8.5	9.1	1.4
Newton	R (Pek)[d]	S	11.2	11.9	8.8	8.5	2.0
PS2465N	R (Pek)	R	9.0	9.1	8.7	8.0	NS
LSD			1.4	1.6	1.4	1.4	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.
[d] R (Pek) = Peking-derived *H. glycines* resistance.

Table 3. Incidence (% of total plants) of stem discoloration after nine weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with artificially infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Cultivar	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g*	LSD[b]
Sturdy	S	S	0	6	50	94	27
BSR101	S	R	0	0	13	75	26
Bell	R (PI88)[c]	S	0	0	6	13	NS
Freeborn	R (PI88)	S	0	0	0	6	NS
Newton	R (Pek)[d]	S	0	0	13	94	15
PS2465N	R (Pek)	R	0	0	0	13	NS
LSD			NS	NS	28	24	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.
[d] R (Pek) = Peking-derived *H. glycines* resistance.

Table 4. Severity (% of stem length discolored) of stem discoloration after nine weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with artificially infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Cultivar	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	S	0	1	9	43	11
BSR101	S	R	0	0	3	43	13
Bell	R (PI88)[c]	S	0	0	2	3	NS
Freeborn	R (PI88)	S	0	0	0	3	NS
Newton	R (Pek)[d]	S	0	0	4	49	9
PS2465N	R (Pek)	R	0	0	0	2	NS
LSD			NS	NS	NS	16	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.
[d] R (Pek) = Peking-derived *H. glycines* resistance.

Table 5. Final *H. glycines* population densities after nine weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with artificially infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Cultivar	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	S	0	89,288	0	113,825	35,231
BSR101	S	R	0	77,775	0	99,475	26,837
Bell	R (PI88)[c]	S	0	4,488	0	4,175	1,864
Freeborn	R (PI88)	S	0	5,863	0	4,238	2,268
Newton	R (Pek)[d]	S	0	775	0	300	539
PS2465N	R (Pek)	R	0	9,475	0	3,200	4,319
LSD			NS	18,719	NS	31,151	

Values presented are eggs per 100 cm^3 potting mix and are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.
[d] R (Pek) = Peking-derived *H. glycines* resistance.

Table 6. Height (mm) of soybean genotypes after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Genotype	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	S	210	163	206	164	24
BSR101	S	R	200	149	219	176	24
Jack	R (PI88)[c]	S	144	147	174	163	NS
Freeborn	R (PI88)	S	180	151	180	175	22
IA1006	S	R	214	188	209	265	NS
IA2008R	S	R	220	155	219	187	40
LSD			40	23	20	NS	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI88.788-derived *H. glycines* resistance.

Table 7. Shoot fresh weight (g) of soybean genotypes after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Genotype	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	S	6.4	3.9	7.4	4.2	1.5
BSR101	S	R	6.3	3.9	8.4	5.1	1.1
Jack	R (PI88)[c]	S	3.9	3.7	6.5	6.3	1.3
Freeborn	R (PI88)	S	6.2	4.5	7.9	6.7	1.0
IA1006	S	R	5.9	3.8	8.4	6.6	1.9
IA2008R	S	R	5.4	3.0	8.0	5.6	1.6
LSD			1.5	NS	0.9	1.1	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.

Table 8. Incidence (% of total plants) of stem discoloration after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Genotype	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g*	LSD[b]
Sturdy	S	S	56	38	38	88	37
BSR101	S	R	0	19	0	81	23
Jack	R (PI88)[c]	S	0	0	6	38	26
Freeborn	R (PI88)	S	0	0	0	44	22
IA1006	S	R	0	0	19	69	21
IA2008R	S	R	0	0	0	81	13
LSD			21	23	23	35	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.

Table 9. Severity (% of stem length discolored) of stem discoloration after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Genotype	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g*	LSD[b]
Sturdy	S	S	9	8	9	49	14
BSR101	S	R	0	5	0	29	9
Jack	R (PI88)[c]	S	0	0	2	8	NS
Freeborn	R (PI88)	S	0	0	0	15	9
IA1006	S	R	0	0	6	23	9
IA2008R	S	R	0	0	0	29	7
LSD			4	6	6	16	

Values presented are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.

Table 10. Final *H. glycines* population densities after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

	Pathogen reaction[a]		Pathogen treatment				
Genotype	*H.g.*	*P.g.*	Control	*H.g.*	*P.g.*	*H.g.+P.g*	LSD[b]
Sturdy	S	S	0	8,025	0	12,338	4,457
BSR101	S	R	0	7,163	0	11,263	3,254
Jack	R (PI88)[c]	S	0	300	0	1,250	1,549
Freeborn	R (PI88)	S	0	488	0	100	304
IA1006	S	R	0	7,263	0	11,775	5,208
IA2008R	S	R	0	5,950	0	10,088	3,247
LSD			NS	3,399	NS	5,611	

Values presented are eggs per 100 cm^3 potting mix and are means of 16 replicate plants.
[a] R = resistant; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.
[c] R (PI88) = PI 88.788-derived *H. glycines* resistance.

Table 11. Height (mm) of soybean genotypes after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

		Pathogen treatment				
Genotype	Resistance[a]	Control	*H.g.*	*P.g.*	*H.g.* + *P.g.*	LSD[b]
Sturdy	S	258	222	219	144	13
BSR101	Rbs3	257	235	211	167	39
Harosoy	S	308	265	241	155	23
L67-6301	Rbs1,3	244	217	208	134	46
L68-0107	Rbs1,3	281	230	221	137	28
LN92-12033	Rbs2	324	289	298	197	70
LN92-12054	S	250	214	218	183	34
LSD		33	35	NS	26	

Values presented are means of 8 replicate plants.
[a] Gene(s) for *P. gregata* resistance; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.

Table 12. Shoot fresh weight (g) of soybean genotypes after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

		Pathogen treatment				
Genotype	Resistance[a]	Control	*H.g.*	*P.g.*	*H.g.* + *P.g.*	LSD[b]
Sturdy	S	8.7	6.8	5.3	0.8	1.2
BSR101	Rbs3	8.0	5.9	5.1	1.2	1.6
Harosoy	S	8.7	7.3	4.9	0.9	1.0
L67-6301	Rbs1,3	7.4	6.3	4.4	1.0	2.3
L68-0107	Rbs1,3	8.1	7.2	4.8	0.8	2.4
LN92-12033	Rbs2	8.5	7.6	4.8	1.6	1.7
LN92-12054	S	8.2	7.1	4.8	1.5	1.7
LSD		NS	NS	NS	0.5	

Values presented are means of 8 replicate plants.
[a] Gene(s) for *P. gregata* resistance; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.

Table 13. Incidence (% of total plants) of stem discoloration after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

		Pathogen treatment				
Genotype	Resistance[a]	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	0	0	100	100	—
BSR101	Rbs3	0	0	0	100	0
Harosoy	S	0	0	13	88	27
L67-6301	Rbs1,3	0	0	38	88	44
L68-0107	Rbs1,3	0	0	25	100	23
LN92-12033	Rbs2	0	0	25	100	40
LN92-12054	S	0	0	0	88	20
LSD		—	—	45	NS	

Values presented are means of 8 replicate plants.
[a] Gene(s) for *P. gregata* resistance; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.

Table 14. Severity (% of stem length discolored) of stem discoloration after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

		Pathogen treatment				
Genotype	Resistance[a]	Control	*H.g.*	*P.g.*	*H.g.+P.g.*	LSD[b]
Sturdy	S	0	0	21	100	2
BSR101	Rbs3	0	0	0	56	13
Harosoy	S	0	0	2	88	20
L67-6301	Rbs1,3	0	0	19	56	29
L68-0107	Rbs1,3	0	0	5	97	6
LN92-12033	Rbs2	0	0	14	52	26
LN92-12054	S	0	0	0	67	25
LSD		—	—	NS	26	

Values presented are means of 8 replicate plants.
[a] Gene(s) for *P. gregata* resistance; S = susceptible.
[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.

Table 15. Final *H. glycines* population densities after eight weeks in a growth chamber experiment with *H. glycines* (*H.g.*) and *P. gregata* (*P.g.*) in four pathogen treatment combinations with naturally infested *P. gregata* straw inoculum.

		Pathogen treatment				
Genotype	Resistance[a]	Control	*H.g.*	*P.g.*	*H.g.* + *P.g.*	LSD[b]
Sturdy	S	0	8,825	0	14,150	7,859
BSR101	Rbs3	0	9,225	0	17,800	9,663
Harosoy	S	0	6,725	0	9,375	6,933
L67-6301	Rbs1,3	0	11,700	0	20,650	7,090
L68-0107	Rbs1,3	0	11,750	0	27,975	10,215
LN92-12033	Rbs2	0	11,875	0	15,550	6,582
LN92-12054	S	0	13,475	0	9,375	10,163
LSD		—	NS	—	NS	

Values presented are eggs per 100 cm^3 potting mix and are means of 8 replicate plants.

[a] Gene(s) for *P. gregata* resistance; S = susceptible.

[b] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.

Table 16. Half-root weight (g), shoot height (Hgt; mm), shoot weight (Wgt; g), incidence (Inc; % total plants) and severity (Sev; % of stem discolored) of stem discoloration characteristic of *P. gregata* (*P.g.*) infection, number of *H. glycines* females (Fem), eggs per female (Eggs/fem), soil and total egg population densities/100 cm^3 potting mix for 'BSR101' soybean in a greenhouse split-root experiment with naturally infested *P. gregata* straw inoculum.

Treatment		Half-root weight			Shoot growth		*P.gregata*		*H. glycines*				
									Per half-root				
A	B	A	B	LSD[a]	Hgt	Wgt	Inc	Sev	Fem	Eggs/fem	Total eggs	Soil[b]	Total/pot
—[c]	—	9.4	10.2	NS	556	20	4	0	---	---	---	---	---
P.g.	—	8.9	9.4	NS	557	18	29	6	---	---	---	---	---
H.g.	—	8.8	9.2	NS	426	17	4	0	12	199	2,078	842	4,406
H.g.	*P.g.*	6.8	7.8	NS	411	17	46	10	10	224	2,053	704	3,843
H.g. + *P.g.*	—	8.6	9.4	NS	456	19	67	18	11	149	1,302	1,058	4,884
LSD		NS	NS		103	NS	22	6	NS	61	NS	NS	NS

Values presented are means of 24 replicate pots.

[a] LSD = Fisher's least significant difference ($P = 0.05$); NS = not significant according to ANOVA.

[b] Final *H. glycines* egg population density per 100 cm^3 potting mix.

[c] — = not infested with *H. glycines* or *P. gregata*.

GENERAL SUMMARY

The first component of the research presented in this dissertation was undertaken to evaluate *Heterodera glycines*-susceptible soybean genotypes for tolerance to parasitism by the nematode and to develop a greenhouse assay for tolerance. Tolerance evaluations based on field experiments were compared to evaluations from greenhouse and growth chamber experiments. The second component of the dissertation investigated the effect of *H. glycines* and *Phialophora gregata*, the causal agent of brown stem rot of soybean, on each other and on soybean growth in greenhouse and growth chamber experiments.

Results of the tolerance experiments revealed *H. glycines*-susceptible soybean genotypes can be evaluated for *H. glycines* tolerance in field experiments without the use of nematicides. Natural variation of *H. glycines* population densities within and among fields provided a range of initial nematode egg population densities (Pi) sufficient to evaluate tolerance based on linear regressions of yield versus nematode population densities. Relative yields [RY=(individual plot yield÷experiment mean yield)×100] were calculated to compensate for differences in yield potential among locations, and $\log_{10}$-transformed Pi [$\text{Log}_{10}(\text{Pi}+1)$] were used to normalize the nematode population data. Linear regression models of RY versus $\text{Log}_{10}(\text{Pi}+1)$ provided a better fit to our data than quadratic or cubic regressions or regressions using nontransformed nematode data.

Significant inverse linear relationships were detected for all genotypes in the

experiment, including a *H. glycines*-resistant genotype, when linear regressions of RY versus $Log_{10}(Pi+1)$ were performed. Linear regression slopes of RY versus $Log_{10}(Pi+1)$ were used as indicators of tolerance, and regression Y intercepts were used as indicators of yield potential in the absence of the nematode. The soybean genotypes evaluated were classified as tolerant, moderately tolerant, and intolerant based on values of linear regression slopes of RY versus $Log_{10}(Pi+1)$. Tolerant soybean genotypes had the least negative values for slope of RY versus $Log_{10}(Pi+1)$, whereas intolerant soybean genotypes had the most negative values for slope. Rank of the linear regression slope values of the genotypes differed between the 1995 and 1996 experiments, and greater variation between years for rank by linear regression slope of RY versus $Log_{10}(Pi+1)$ was observed among soybean genotypes classed as moderately tolerant than among those classed as either tolerant or intolerant.

Evaluation of tolerance using regression slopes of yield versus nematode population densities required sampling and processing soil from each plot in the experiment. Such a method of tolerance determination is not practical for evaluating a large number of soybean lines. Tolerance indices (TI=(mean relative yield in *H. glycines*-infested fields÷mean relative yield in noninfested fields)×100] were calculated as an alternative method of tolerance determination, and TI correlated well to linear regression slopes of RY versus $Log_{10}(Pi+1)$ in both years of the experiment. The calculation of TI is a less labor intensive method of tolerance evaluation, and would be more adaptable for screening large numbers of genotypes than would evaluations based on the regression analysis described above.

Yield loss attributable to nematode parasitism was detected not only in *H. glycines*-susceptible genotypes. Relative yield of the *H. glycines*-resistant genotype included in the experiment decreased as *H. glycines* population densities increased, supporting previous research detecting yield reductions of *H. glycines*-resistant cultivars as nematode population densities increase. Additionally, yield loss attributable to nematode parasitism of a *H. glycines*-resistant cultivar in heavily infested fields supports the concept that tolerance and resistance are independent soybean characteristics.

In both years of the experiment, the most tolerant soybean genotypes had RY values less than the *H. glycines*-resistant and moderately tolerant genotypes across all Pi levels, and a moderately tolerant genotype had RY greater than the *H. glycines*-resistant genotype at low to moderate Pi levels. Results indicate that maximum yields in soils infested with low to moderate levels of *H. glycines* may be obtained by growing high-yielding, moderately tolerant, *H. glycines*-susceptible soybean genotypes.

Linear regression analyses of plant height and weight versus Pi revealed few significant relationships when the genotypes included in the field experiment were grown in a greenhouse experiment in potting soil infested with a range of *H. glycines* population densities. Environmental conditions in the greenhouse room may have contributed to the lack of detection of significant relationships. Therefore, similar experiments were conducted in a growth chamber with genotypes selected from the field experiment. Significant inverse relationships were detected when linear regressions of plant growth after eight weeks versus Pi were performed, however, the results did not correlate with those of the field experiment. In fact, the most and least tolerant

genotypes based on the field experiments had the most negative and least negative values (respectively) for slope of plant growth versus Pi in the growth chamber experiment. The lack of agreement between field, greenhouse, and growth chamber evaluations and amount of labor required for field evaluation of tolerance suggests screening large numbers of genotypes in a soybean breeding program for *H. glycines* tolerance may not be feasible.

The second component of the described research investigated the effect of *H. glycines* and *P. gregata* on each other and on soybean growth in greenhouse and growth chamber experiments. Incidence and severity of soybean stem discoloration characteristic of *P. gregata* infection was greater in soil infested with both pathogens than in soil infested with *P. gregata* alone. The increased incidence and severity occurred for all *H. glycines*-susceptible soybean genotypes and for a 'Peking'-derived *H. glycines*-resistant, *P. gregata*-susceptible cultivar. However, increased incidence was not observed with PI 88.788-derived *H. glycines* resistant, *P. gregata*-susceptible or a 'Peking'-derived *H. glycines*-resistant, *P. gregata*-resistant soybean cultivars.

The effects of the different pathogen treatments on soybean growth were not consistent among experiments and genotypes. Plant height, root weight, and shoot weight generally were suppressed when plants were grown in pathogen-infested potting mix, but no consistent trend was revealed by analysis of the data.

A split-root experiment was conducted to determine whether the increase in stem discoloration was a systemic phenomenon. We observed a consistent increase in incidence of stem discoloration when *H. glycines* and *P. gregata* were inoculated on

separate half-root systems than when half-roots were inoculated with *P. gregata* alone, but the increase was not significant at $P=0.05$. Fewer eggs per female were produced in single pots containing both pathogens than in single pots where the two pathogens were physically separated, although, no differences in total soil egg population densities after eight weeks were detected in any of our experiments.

Our experiments did not attempt to elucidate specific mechanisms of the interaction between the two pathogens nor the effects of the interaction between the two pathogens on soybean yield. Field experiments would be required to adequately asses effects of the pathogen combinations on soybean growth and yield. We suggest resistance to both pathogens is necessary to minimize *P. gregata* infection of soybean when both pathogens are present, and that *H. glycines*-free fields are required for evaluation of soybean genotypes for *P. gregata* reaction.

In summary, the research described herein revealed that soybean genotypes can be evaluated for tolerance to parasitism by *H. glycines* in fields naturally infested with the nematode without using nematicides. Additionally, tolerance evaluations based on calculation of tolerance indices required less labor than evaluations based on regression analysis, although, without a suitable greenhouse assay, the evaluation of large numbers of genotypes may not be feasible. Our results also suggest that high-yielding, moderately tolerant, *H. glycines*-susceptible soybean genotypes may provide yields equal to or greater than *H. glycines*-resistant genotypes across a range of nematode population densities without exerting selection pressure on the nematode populations. The described research also substantiates observations of greater brown stem rot symptom

development in soybean plants grown in soils infested with both *H. glycines* and *P. gregata* than in soils infested with *P. gregata* alone. A combination of resistance to both pathogens is recommended when soybean is planted in fields infested with both pathogens, and evaluations of soybean genotypes for *P. gregata* reaction should be conducted in fields free of the nematode.

APPENDIX

Table A-1. Soil characteristics of the 1994 field experiment locations.

			Texture Analysis (%)					
Location	Race	Pi†	Clay	Sand	Silt	Soil class	O.M.(%)	pH
Ames	3	1736	33.0	29.4	37.6	Clay loam	5.5	7.6
Colo	3	1879	33.0	27.8	39.2	Clay loam	5.2	7.4
Kanawha	3	1771	35.0	27.4	37.6	Clay loam	5.4	7.0
Nevada	6	5569	27.0	41.4	31.6	Loam-clay loam	4.1	7.4

† Pi = initial SCN population density (eggs 100^{-1} cm^{-3} soil) determined at planting. Values presented are means of 120 plots at each location.

Table A-2. Planting, harvest, and soil sampling dates for the 1994 field experiment.

			Sample dates		
Location	Plant Date	Harvest Date	Initial	R2†	Final
Ames	3 May	12 October	4 & 5 May	29 June (N)‡	9 September (N)
				6 July (C)	20 September (C)
				12 July (S)	29 September (S)
Colo	4 May	30 September	5 May	29 June (N)	13 September (N)
				12 July (C)	21 September (C)
				18 July (S)	29 September (S)
Kanawha	9 May	14 October	10 May	7 July (N)	5 October (all)
				15 July (C&S)	
Nevada	12 May	30 September	16 May	30 June (N)	9 September (N)
				12 July (C)	18 September (C)
				18 July (S)	30 September (S)

† R2 = reproductive stage R2; full bloom (Fehr et al., 1971).
‡ Maturity sets: N = north; C = central; S = south.

Table A-3. Brown stem rot (BSR), Phytophthora root rot (PRR), and iron deficiency chlorosis (IDC) ratings for soybean genotypes included in the 1994 field experiment.

Maturity	Genotype	BSR†	PRR‡	PRR Tol§	IDC¶
North	Bell (R)#	S	S	3.3	2.3
	Agripro AP1989	S	Rps1c	2.1	3.3
	Agripro AP1993	S	S	1.8	3.5
	BSR101	R	Rps1a	3.2	2.1
	IA1004	S	—	—	—
	Marcus BC	S	Rps1k,6	4.2	4.3
	Northrup-King S19-90	S	Rps1c	3.7	2.7
	Northrup-King S20-20	S	Rps1c	3.3	2.2
	Parker	S	Rps1a	3.1	3.0
	Sturdy	S	Rps1a	3.1	2.2
Central	Jack (R)	S	S	3.6	2.7
	Agripro AP3035	S	S	1.9	4.2
	IA2007	S	Rps1c	3.7	4.4
	IA2008	R	S	3.6	3.3
	Kenwood	S	S	3.1	3.4
	Northrup-King S24-92	S	S	3.2	4.4
	Northrup-King S28-01	S	Rps1c	3.9	3.7
	Pioneer P9272	S	S	2.3	3.7
	Pioneer P9273	S	S	3.7	2.6
	Pioneer P9381	S	S	3.2	3.7
South	Yale (R)	S	S	—	—
	A92-727017	S	S	4.0	4.7
	C1832	S	Rps1k	4.2	4.7
	Northrup-King S30-06	S	S	3.2	3.1
	Northrup-King S35-35	S	Rps1c	2.8	2.4
	Pioneer P9303	S	S	3.6	3.4
	Pioneer P9341	S	S	3.9	3.0
	Pioneer P9381	S	S	3.2	3.7
	Pioneer P9392	S	S	3.4	2.4
	Sherman	S	S	3.8	3.4

† Brown stem rot (R = resistant; S = susceptible).

‡ Genes for resistance to Phytophthora root rot; S =susceptible.

§ Greenhouse evaluation of field tolerance to Phytophthora root rot taken from Iowa soybean yield test reports (Iowa State University Extension. AG 18-5. Ames.) from 1991 to 1993. Ratings are on a scale of 1 = no dead plants or stunting to 5 = all plants dead.

¶ Iron deficiency chlorosis ratings taken from Iowa soybean yield test reports (Iowa State University Extension. AG 18-5. Ames. from 1991 to 1993. Ratings are on a scale of 1 = little or no yellowing to 5 = very severe yellowing.

R = SCN-resistant.

Table A-4. Initial SCN population densities for the 1994 field experiment, by maturity set, genotype, and location.

		Location			
Maturity	Genotype	Ames	Colo	Kanawha	Nevada
North	Bell (R)†	625	912	1875	2 263
	AP1989	375	638	2025	2 838
	AP1993	963	1875	1750	4 225
	BSR101	413	913	1163	3 525
	IA1004	350	1450	1313	3 213
	Marcus BC	725	988	1175	2 750
	S19-90	850	937	1175	3 300
	S20-20	438	738	1400	3 775
	Parker	700	913	1588	3 963
	Sturdy	550	700	938	1 888
	LSD(0.05)	NS‡	NS	NS	NS
Central	Jack (R)	2112	1813	2300	9 488
	AP3035	2025	1375	2838	8 900
	IA2007	1988	3450	1975	8 900
	IA2008	2450	2238	1700	6 275
	Kenwood	2825	1675	2775	4 150
	S24-92	2088	2413	1825	6 388
	S28-01	2088	2575	2288	8 513
	P9272	2788	2025	2550	6 913
	P9273	1488	1913	1738	9 738
	P9381	1975	1400	1488	7 413
	LSD(0.05)	NS	NS	NS	NS
South	Yale (R)	1700	1788	1313	4 538
	A92-727017	2188	2963	1538	6 450
	Probst	2838	3125	2113	10 388
	S30-06	3650	2650	1725	4 713
	S35-35	1638	2663	1350	3 300
	P9303	2275	2363	2013	5 825
	P9341	2500	2613	2075	6 875
	P9381	2163	2400	2100	6 200
	P9392	2388	3225	1750	4 850
	Sherman	2925	1650	1300	5 525
	LSD(0.05)	NS	NS	NS	3651

Values presented are eggs 100^{-1} cm^{-3} soil and are means of four replications per location.

† R = SCN-resistant.

‡ NS = not significant.

Table A-5. Mid-season SCN population densities for the 1994 field experiment, by maturity set, genotype, and location.

		Location			
Maturity	Genotype	Ames	Colo	Kanawha	Nevada
North	Bell (R)†	113	1225	488	1 338
	AP1989	2 275	2413	1938	3 075
	AP1993	4 075	2375	2063	6 850
	BSR101	1 400	1488	1825	6 325
	IA1004	1 225	2425	2125	3 375
	Marcus BC	3 700	2675	2175	6 850
	S19-90	2 237	1588	1763	6 800
	S20-20	2 725	1888	2375	5 400
	Parker	2 200	2550	2475	4 300
	Sturdy	1 625	2338	2388	4 475
	LSD(0.05)	1 740	NS‡	NS	NS
Central	Jack (R)	900	550	1038	2 000
	AP3035	5 850	6925	3250	8 250
	IA2007	4 975	3450	2700	12 550
	IA2008	5 050	5475	2375	7 725
	Kenwood	5 025	3125	2025	13 700
	S24-92	3 550	3175	1850	7 050
	S28-01	4 475	4750	2650	8 250
	P9272	5 775	5900	2000	8 975
	P9273	5 825	4350	2175	8 500
	P9381	3 825	4275	2675	9 825
	LSD(0.05)	2 666	NS	NS	4 827
South	Yale (R)	862	613	563	1 675
	A92-727017	5 900	3850	1563	7 325
	Probst	5 800	6575	1675	5 275
	S30-06	12 175	6000	2750	11 850
	S35-35	9 775	7725	1788	9 025
	P9303	4 375	5250	1263	9 025
	P9341	8 375	5375	1450	7 325
	P9381	7 275	5200	2700	6 650
	P9392	5 650	6200	1462	4 925
	Sherman	8 600	2775	2225	8 025
	LSD(0.05)	3777	3074	1104	3460

Values presented are eggs 100^{-1} cm^{-3} soil and are means of four replications each.
† R = SCN-resistant.
‡ NS = not significant.

Table A-6. Final SCN population densities for the 1994 field experiment, by maturity set, genotype, and location.

		Location			
Maturity	Genotype	Ames	Colo	Kanawha	Nevada
North	Bell (R)†	262	1 413	1750	4 025
	AP1989	11 250	29 950	3800	16 750
	AP1993	17 325	21 475	6650	27 550
	BSR101	17 100	15 700	6900	16 425
	IA1004	10 150	24 400	5375	21 650
	Marcus BC	20 975	35 500	8250	25 925
	S19-90	11 950	23 550	7250	19 775
	S20-20	12 300	21 925	7900	23 425
	Parker	14 725	25 450	7500	21 125
	Sturdy	19 300	18 975	7250	27 025
	LSD(0.05)	5 857	17 123	4392	11 273
Central	Jack (R)	938	1 088	2288	2 825
	AP3035	25 525	23 700	6500	38 750
	IA2007	29 650	19 200	5175	27 800
	IA2008	27 625	14 675	6050	20 925
	Kenwood	33 325	10 125	4825	37 525
	S24-92	20 950	16 700	5075	31 425
	S28-01	30 450	17 475	5050	19 175
	P9272	23 800	19 725	4900	28 525
	P9273	28 850	23 125	4975	24 425
	P9381	19 350	17 650	5150	18 400
	LSD(0.05)	15 073	12 977	NS‡	11 537
South	Yale (R)	1 588	800	900	3 875
	A92-727017	36 925	12 200	5925	17 400
	Probst	32 350	22 550	6650	27 500
	S30-06	45 075	10 925	8600	23 475
	S35-35	35 025	10 850	5525	24 100
	P9303	27 125	14 400	6700	26 075
	P9341	34 300	11 825	7600	24 625
	P9381	23 700	12 975	5175	16 900
	P9392	27 700	16 250	5550	14 550
	Sherman	34 225	11 700	8175	20 225
	LSD(0.05)	12 819	8563	3346	11 501

Values presented are eggs 100^{-1} cm^{-3} soil and are means of four replications each.
† R = SCN-resistant.
‡ NS = not significant.

Table A-7. Reproductive factors† for soybean genotypes included in the 1994 field experiment, by maturity set, genotype, and location.

		Location				
Maturity	Genotype	Ames	Colo	Kanawha	Nevada	Mean
North	Bell (R)‡	0.6	1.6	3.0	3.0	2.0
	AP1989	50.6	45.8	2.2	9.2	26.9
	AP1993	20.1	16.1	4.7	8.9	12.5
	BSR101	44.8	29.3	12.9	14.0	25.3
	IA1004	33.5	30.6	4.5	7.1	18.9
	Marcus BC	68.7	192.0	9.4	11.1	70.3
	S19-90	35.3	44.6	8.0	10.0	24.5
	S20-20	49.6	54.3	6.2	8.8	29.7
	Parker	36.7	30.1	5.8	11.3	20.9
	Sturdy	49.3	29.9	33.0	15.8	32.0
	LSD(0.05)	NS§	NS	NS	NS	37.5
Central	Jack(R)	0.7	0.6	1.8	0.3	0.9
	AP3035	12.8	39.7	3.0	6.3	15.5
	IA2007	23.5	7.3	3.2	3.3	9.4
	IA2008	13.8	10.6	10.2	3.4	9.5
	Kenwood	18.2	5.7	2.0	8.9	8.7
	S24-92	14.1	6.9	2.9	6.7	7.6
	S28-01	26.0	7.0	2.3	2.6	9.5
	P9272	10.9	10.9	4.3	5.1	7.8
	P9273	51.4	13.8	3.9	2.7	17.9
	P9381	11.2	15.6	3.8	2.6	8.3
	LSD(0.05)	NS	NS	NS	3.6	NS
South	Yale (R)	0.9	0.5	0.9	1.0	0.8
	A92-727017	26.1	4.5	4.3	4.2	9.8
	Probst	11.4	8.7	3.6	2.6	6.6
	S30-06	13.1	4.5	6.3	5.9	7.4
	S35-35	23.9	4.9	4.8	8.1	10.4
	P9303	13.7	6.5	4.9	5.2	7.6
	P9341	14.6	6.7	3.9	3.6	6.9
	P9381	10.8	6.0	3.3	3.0	5.8
	P9392	12.7	6.0	4.0	3.6	6.6
	Sherman	11.6	11.4	6..2	4.9	8.5
	LSD(0.05)	13.3	NS	NS	NS	5.0

Values presented are means of four replications each.

† Reproductive factor = final SCN population density÷initial SCN population density.

‡ R = SCN-resistant.

§ NS = not significant.

Table A-8. Yield of soybean genotypes included in the 1994 field experiment, by maturity set, genotype, and location.

		Location					
Maturity	Genotype	Ames	Colo	Kanawha	Nevada	Mean	Rank
North	AP1989	3053	3314	2304	2453	2781	8
	AP1993	3189	3752	2354	2180	2869	5
	Bell (R)†	4016	3976	3329	2852	3543	1
	BSR101	3275	3588	2722	1993	2895	3
	IA2004	3692	3702	2537	2284	3054	2
	Marcus BC	3107	3712	2270	1990	2770	9
	S19-90	3305	3189	2707	2324	2881	4
	S20-20	3127	3364	2287	2460	2810	7
	Parker	3236	3089	2220	2282	2707	10
	Sturdy	3132	3806	2131	2257	2832	6
	Mean	3313	3549	2486	2308	2914	
	LSD(0.05)	475	562	300	488	453	
Central	AP3035	3635	2993	3228	2460	3079	5
	IA2007	3122	3576	2596	2327	2905	9
	IA2008	3315	3391	3297	2529	3133	4
	Jack (R)	4280	4080	3786	3357	3876	1
	Kenwood	3425	3284	2867	2332	2977	7
	S24-92	3410	3791	3203	2494	3225	2
	S28-01	3447	3376	2737	2600	3040	6
	P9272	3295	3016	2988	2181	2870	10
	P9273	3532	3598	3073	2536	3185	3
	P9381	3389	3090	2485	2741	2926	8
	Mean	3485	3420	3026	2556	3122	
	LSD(0.05)	445	709	281	257	355	
South	A92-727017	3396	3480	2979	3368	3306	6
	C1832	3749	3647	3396	3001	3448	2
	S30-06	3173	3808	2736	2803	3130	10
	S35-35	3509	3924	3048	3124	3401	3
	P9303	3351	3867	2808	2995	3255	7
	P9341	3364	3927	2665	2835	3198	8
	P9381	3063	3626	2926	3011	3157	9
	P9392	3386	3546	3161	3299	3348	4
	Sherman	3939	3410	2737	3284	3343	5
	Yale (R)	4278	4411	3305	3818	3953	1
	Mean	3521	3765	2976	3154	3354	
	LSD(0.05)	372	707	414	369	342	

Values presented are kg ha^{-1} adjusted to 13.5% moisture and are means of four replications each.
† R = SCN-resistant.

Table A-9. Results of linear regression analysis of relative yield† (RY) versus log_{10}-transformed initial SCN population densities [eggs 100^{-1} cm^{-3} soil; $Log_{10}(Pi+1)$] for the 1994 field experiment.

		Mean				
Maturity	Genotype	RY	$Log_{10}(Pi+1)$	Slope	Y intercept	R^2
North	Bell (R)‡	121.6	3.0	-20.86 NS	183.7	0.20
	S19-90	98.9	3.0	-21.11 *	162.4	0.36
	BSR101	99.4	3.0	-21.63 NS	163.4	0.15
	Sturdy	97.2	2.9	-22.27 NS	161.6	0.10
	Marcus BC	95.1	2.9	-23.44 NS	163.8	0.17
	AP1989	95.5	3.0	-23.98 **	166.3	0.42
	S20-20	96.4	3.0	-23.99 *	168.1	0.34
	Parker	92.9	3.1	-28.39 *	179.8	0.36
	IA1004	104.8	3.0	-28.47 *	190.4	0.29
	AP1993	98.5	3.2	-28.54 NS	190.5	0.12
	LSD(0.05)	15.6	NS§			
Central	P9381	93.7	3.3	-3.70 NS	106.1	0.01
	IA2007	93.1	3.5	-10.14 NS	128.4	0.04
	IA2008	100.4	3.4	-14.70 NS	150.1	0.17
	AP3035	98.6	3.4	-17.61 NS	158.4	0.21
	S28-01	97.4	3.4	-18.07 NS	159.7	0.16
	Jack (R)	124.2	3.4	-18.06 *	186.1	0.29
	P9272	91.9	3.4	-20.35 NS	161.6	0.23
	P9273	102.0	3.3	-24.86 **	185.1	0.57
	S24-92	103.3	3.4	-31.90 *	211.5	0.31
	Kenwood	95.4	3.4	-42.72 *	240.5	0.32
	LSD(0.05)	11.4	NS			
South	Sherman	99.7	3.3	35.60 *	-19.4	0.25
	S30-06	93.3	3.4	9.34 NS	61.1	0.02
	S35-35	101.4	3.3	5.55 NS	83.2	0.01
	Yale (R)	117.9	3.3	4.14 NS	104.3	0.01
	P9392	99.8	3.4	1.11 NS	96.0	0.00
	A92-727017	98.6	3.4	-0.13 NS	99.0	0.00
	P9303	97.1	3.4	-6.59 NS	119.5	0.02
	P9341	95.3	3.5	-10.61 NS	132.2	0.02
	C1832	102.8	3.5	-11.20 NS	142.3	0.12
	P9381	94.1	3.4	-12.02 NS	135.9	0.07
	LSD(0.05)	10.2	NS			

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† RY = (individual plot yield ÷ experiment mean yield) × 100.

‡ R = SCN-resistant.

§ NS = not significant.

Table A-10. Results of linear regression analysis of relative yield† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at R2‡ [Log_{10}(PR2+1)] and R8 [Log_{10}(Pf+1)] growth stages for the 1994 field experiment.

		Log_{10}(PR2+1)			Log_{10}(Pf+1)		
Maturity	Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2
North	AP1989	-20.64 NS#	163.8	0.11	20.75 NS	11.6	0.23
	AP1993	-20.64 NS	202.5	0.08	5.93 NS	73.7	0.00
	Bell (R)§	-15.18 NS	162.3	0.18	-24.22 **	195.9	0.43
	BSR101	-48.49 **	259.0	0.57	5.13 NS	48.4	0.00
	IA1004	-31.58 NS	207.4	0.21	8.70 NS	69.4	0.02
	Marcus BC	-30.64 *	199.4	0.25	27.98 NS	-24.6	0.08
	Parker	-27.79 NS	187.4	0.12	26.91 NS	-19.3	0.14
	S19-90	-24.53 *	180.6	0.39	7.01 NS	69.9	0.01
	S20-20	-33.21 **	209.6	0.28	33.28 *	-41.3	0.25
	Sturdy	-22.74 NS	173.2	0.07	20.22 NS	12.6	0.05
Central	AP3035	-15.39 NS	156.0	0.05	-18.62 NS	178.0	0.16
	IA2007	-3.04 *	202.9	0.29	1.55 NS	86.5	0.00
	IA2008	-16.71 NS	161.5	0.09	-16.01 NS	166.7	0.15
	Jack (R)	-27.04 *	204.3	0.31	-25.16 *	203.7	0.31
	Kenwood	-30.73 *	207.4	0.31	-12.58 NS	147.7	0.09
	P9272	-16.13 NS	150.9	0.10	-16.05 NS	159.1	0.13
	P9273	-16.92 NS	163.8	0.08	3.87 NS	85.8	0.01
	P9381	7.66 NS	66.1	0.03	16.64 NS	25.4	0.11
	S24-92	-20.09 NS	173.2	0.13	-19.23 NS	183.4	0.13
	S28-01	-15.34 NS	153.1	0.07	15.67 NS	32.5	0.11
South	A92-727017	10.91 NS	59.6	0.13	5.73 NS	74.8	0.04
	C1832	-1.62 NS	108.6	0.00	4.53 NS	83.6	0.02
	P9303	6.87 NS	72.6	0.04	7.24 NS	66.8	0.03
	P9341	15.62 NS	38.5	0.12	-4.54 NS	114.4	0.01
	P9381	-2.28 NS	102.5	0.00	2.62 NS	83.4	0.00
	P9392	14.55 *	47.6	0.27	4.30 NS	82.1	0.02
	S30-06	-0.15 NS	93.9	0.00	-5.02 NS	114.5	0.01
	S35-35	10.32 NS	62.7	0.07	1.87 NS	93.7	0.00
	Sherman	29.94 NS	9.2	0.16	26.98 NS	-13.0	0.13
	Yale (R)	-3.79 NS	128.8	0.00	-9.10 NS	145.9	0.07

* , ** significant at the 0.05 and 0.01 probability level, respectively.

† Relative yield = (individual plot yield÷experiment mean yield)×100.

‡ R2 and R8 = full bloom and harvest maturity, respectively (Fehr et al., 1971).

¶ R = SCN-resistant.

NS = not significant.

Table A-11. Results of linear regression analysis of relative plant height† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at planting [Log_{10}(Pi+1)], R2‡ [Log_{10}(PR2+1)], and harvest [Log_{10}(Pf+1)] for the 1994 field experiment, north maturity set.

	Log_{10}(Pi+1)			Log_{10}(PR2+1)			Log_{10}Pf+1)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP1989	-2.54 NS§	108.6	0.03	-0.23 NS	101.9	0.00	7.09 NS	72.4	0.17
AP1993	-13.49 *	134.8	0.31	-3.61 NS	104.0	0.01	-0.03 NS	91.5	0.00
Bell (R)¶	-0.67 NS	102.0	0.00	-0.85 NS	102.3	0.01	1.68 NS	94.9	0.04
BSR101	-8.64 *	129.6	0.30	-11.59 **	142.2	0.41	5.68 NS	80.8	0.05
IA1004	-5.25 NS	111.6	0.15	-5.14 NS	112.6	0.09	-1.77 NS	103.1	0.01
Marcus BC	0.18 NS	97.9	0.00	-0.28 NS	99.4	0.00	1.51 NS	91.9	0.00
S19-90	-1.97 NS	98.5	0.01	-3.20 NS	103.3	0.03	-1.99 NS	100.8	0.00
S20-20	-3.96 NS	114.9	0.07	1.92 NS	96.6	0.01	5.22 NS	81.5	0.04
Parker	1.18 NS	103.3	0.00	10.41 NS	71.5	0.10	8.00 NS	73.6	0.08
Sturdy	-8.09 NS	129.8	0.15	-15.25 *	157.3	0.38	-3.89 NS	122.7	0.02

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Relative plant height = (plot plant height÷experiment mean plant height)×100.

‡ R2 = full bloom (Fehr et al., 1971).

§ NS = not significant.

¶ R = SCN-resistant.

Table A-12. Results of linear regression analysis of relative plant height† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at planting [Log_{10}(Pi+1)], R2‡ [Log_{10}(PR2+1)], and harvest [Log_{10}(Pf+1)] for the 1994 field experiment, central maturity set.

	Log_{10}(Pi+1)			Log_{10}(PR2+1)			Log_{10}Pf+1)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP3035	-2.46 NS§	103.6	0.04	-7.32 NS	122.5	0.12	-6.18 NS	121.6	0.17
IA2007	-5.70 NS	122.1	0.06	-14.62 *	155.6	0.34	-14.20 *	161.9	0.33
IA2008	-1.18 NS	111.6	0.00	-5.85 NS	129.0	0.03	-11.95 NS	157.0	0.21
Jack (R)¶	21.41 *	46.4	0.34	20.38 NS	59.5	0.15	16.29 NS	68.4	0.11
Kenwood	-7.02 NS	126.5	0.06	-5.64 NS	123.3	0.07	-6.34 NS	129.1	0.15
S24-92	-0.83 NS	94.7	0.00	-3.35 NS	103.6	0.03	-3.07 NS	104.7	0.03
S28-01	-3.70 NS	105.7	0.02	-9.91 NS	128.9	0.10	-5.26 NS	114.8	0.05
P9272	4.23 NS	78.7	0.07	-5.84 NS	114.5	0.09	-0.28 NS	94.3	0.00
P9273	-4.92 NS	111.0	0.19	-2.82 NS	104.8	0.02	-4.37 NS	112.9	0.08
P9381	2.88 NS	90.4	0.03	1.22 NS	95.7	0.00	-5.49 NS	122.6	0.08

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Relative plant height = (plot plant height÷experiment mean plant height)×100.

‡ R2 = full bloom (Fehr et al., 1971).

§ NS = not significant.

¶ R = SCN-resistant.

Table A-13. Results of linear regression analyses of relative plant height† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at planting [Log_{10}(Pi+1)], R2‡ [Log_{10}(PR2+1)], and harvest [Log_{10}(Pf+1)] for the 1994 field experiment, south maturity set.

	Log_{10}(Pi+1)			Log_{10}(PR2+1)			Log_{10}Pf+1)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
A92-727017	-3.61 NS§	117.4	0.02	-1.62 NS	110.9	0.00	-6.52 NS	132.1	0.09
C1832	2.13 NS	91.9	0.01	-16.38 **	158.5	0.41	-9.79 NS	140.8	0.22
S30-06	-10.69 NS	134.3	0.09	-18.11 **	166.7	0.48	-18.17 **	174.4	0.46
S35-35	-6.22 NS	117.8	0.03	-13.28 *	147.1	0.28	-15.38 **	161.2	0.39
P9303	1.75 NS	88.1	0.01	-1.24 NS	98.5	0.01	-4.52 NS	113.0	0.08
P9341	1.59 NS	94.0	0.00	-13.52 *	148.8	0.33	-15.81 *	165.8	0.36
P9381	8.49 NS	66.0	0.10	-8.47 NS	126.2	0.08	-11.76 NS	143.2	0.20
P9392	-0.66 NS	106.3	0.00	-9.08 NS	136.6	0.13	-14.70 *	164.6	0.35
Sherman	5.89 NS	80.2	0.08	6.13 NS	77.6	0.07	-1.74 NS	107.1	0.01
Yale (R)¶	6.79 NS	86.1	0.15	7.73 NS	85.9	0.13	7.39 *	85.4	0.28

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Relative plant height = (plot plant height÷experiment mean plant height)×100.

‡ R2 = full bloom (Fehr et al., 1971).

§ NS = not significant.

¶ R = SCN-resistant.

Table A-14. Results of linear regression analysis of relative seed weight† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at planting [Log_{10}(Pi+1)], R2‡ [Log_{10}(PR2+1)], and harvest [Log_{10}(Pf+1)] for the 1994 field experiment, north maturity set.

	Log_{10}(Pi+1)			Log_{10}(PR2+1)			Log_{10}Pf+1)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP1989	0.42 NS§	91.8	0.00	2.57 NS	84.5	0.01	10.09 *	52.2	0.34
AP1993	7.54 NS	80.3	0.07	15.92 NS	48.8	0.19	8.88 NS	67.6	0.08
Bell (R)¶	1.43 NS	104.5	0.02	2.45 NS	102.2	0.11	2.07 NS	102.4	0.08
BSR101	8.11 *	69.9	0.30	6.23 NS	73.4	0.13	5.61 NS	71.0	0.05
IA1004	5.24 NS	84.0	0.17	5.11 NS	83.2	0.09	7.52 NS	69.2	0.20
Marcus BC	2.80 NS	85.8	0.05	-1.62 NS	99.5	0.01	11.47 *	45.0	0.25
S19-90	4.00 NS	94.8	0.12	3.91 NS	93.9	0.09	1.61 NS	100.2	0.01
S20-20	6.59 NS	83.1	0.14	5.17 NS	85.2	0.04	22.09 **	11.4	0.63
Parker	9.73 NS	66.0	0.20	18.10 NS	34.2	0.25	2.63 NS	84.8	0.01
Sturdy	9.30 NS	71.0	0.10	11.16 NS	60.6	0.10	25.92 **	-10.5	0.43

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Seed weight = g 100^{-1} $seeds^{-1}$; Relative seed weight = (individual plot seed weight÷experiment mean seed weight)×100.

‡ R2 = full bloom (Fehr et al., 1971).

§ NS = not significant.

¶ R = SCN-resistant.

Table A-15. Results of linear regression analysis of relative seed weight† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at planting [Log_{10}(Pi+1)], R2‡ [Log_{10}(PR2+1)], and harvest [Log_{10}(Pf+1)] for the 1994 field experiment, central maturity set.

	Log_{10}(Pi+1)			Log_{10}(PR2+1)			Log_{10}Pf+1)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP3035	3.28 NS§	90.7	0.06	6.98 NS	75.8	0.09	5.32 NS	79.1	0.11
IA2007	1.46 NS	108.6	0.00	2.51 NS	104.6	0.01	16.57 **	44.1	0.54
IA2008	7.55 *	66.4	0.33	13.18 **	43.7	0.42	6.30 NS	65.8	0.17
Jack (R)¶	3.91 NS	86.8	0.10	1.33 NS	96.3	0.01	3.37 NS	89.6	0.04
Kenwood	-1.45 NS	103.6	0.01	3.34 NS	86.5	0.07	2.97 NS	86.3	0.10
S24-92	4.10 NS	81.3	0.20	1.10 NS	91.4	0.02	2.40 NS	85.2	0.08
S28-01	8.30 NS	70.7	0.17	17.55 **	35.7	0.43	15.23 **	36.3	0.53
P9272	7.07 NS	80.0	0.21	5.20 NS	85.1	0.08	7.02 NS	74.8	0.18
P9273	3.47 NS	87.3	0.13	12.92 **	51.8	0.54	10.17 **	56.3	0.63
P9381	12.05 *	54.0	0.31	13.19 *	46.8	0.29	20.19 **	11.5	0.61

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Seed weight = g 100^{-1} $seeds^{-1}$; Relative seed weight = (individual plot seed weight÷experiment mean seed weight)×100.

‡ R2 = full bloom (Fehr et al., 1971).

§ NS = not significant.

¶ R = SCN-resistant.

Table A-16. Results of linear regression analysis of relative seed weight† versus log_{10}-transformed SCN population densities (eggs 100^{-1} cm^{-3} soil) at planting [Log_{10}(Pi+1)], R2‡ [Log_{10}(PR2+1)], and harvest [Log_{10}(Pf+1)] for the 1994 field experiment, south maturity set.

	Log_{10}(Pi+1)			Log_{10}(PR2+1)			Log_{10}Pf+1)		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
A92-727017	5.04 NS§	82.4	0.09	12.34 **	55.4	0.50	7.92 NS	66.7	0.23
C1832	2.81 NS	89.5	0.06	5.44 NS	79.7	0.13	6.09 *	73.6	0.26
S30-06	11.38 NS	67.7	0.16	10.79 *	65.7	0.28	6.21 NS	80.7	0.09
S35-35	6.74 NS	80.7	0.09	6.01 NS	80.4	0.15	9.09 *	65.2	0.34
P9303	22.40 *	33.0	0.32	24.92 **	20.4	0.73	31.91 **	-24.1	0.68
P9341	4.20 NS	76.7	0.04	9.39 **	57.2	0.41	7.80 NS	58.7	0.22
P9381	16.35 **	36.6	0.40	11.87 NS	48.9	0.17	12.70 *	40.7	0.27
P9392	4.06 NS	82.5	0.07	7.85 *	68.1	0.33	4.24 NS	78.9	0.10
Sherman	22.50 **	27.1	0.53	23.46 **	17.0	0.51	17.79 *	28.0	0.30
Yale (R)¶	4.59 NS	84.4	0.18	4.91 NS	85.1	0.14	1.34 NS	95.1	0.02

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† Seed weight = g 100^{-1} $seeds^{-1}$; Relative seed weight = (individual plot seed weight÷experiment mean seed weight)×100.

‡ R2 = full bloom (Fehr et al., 1971).

§ NS = not significant.

¶ R = SCN-resistant.

Table A-17. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed initial SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, north maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP1989	-8.45 **	72.0	0.87	-3.79 **	131.3	0.54	3.45 *	62.7	0.57
AP1993	-7.59 **	76.9	0.79	-8.94 **	150.7	0.79	-2.06 NS	76.0	0.36
Bell (R)‡	-8.54 NS§	74.4	0.33	-4.11 NS	138.9	0.14	-0.04 NS	75.9	0.00
BSR101	-6.67 NS	69.7	0.38	-5.37 *	140.0	0.35	0.12 NS	72.1	0.00
IA1004	-4.62 **	59.4	0.92	-6.04 **	139.9	0.73	-2.34 *	83.0	0.59
Marcus BC	-4.82 *	66.6	0.58	-4.06 NS	136.2	0.31	-1.02 NS	74.7	0.48
Parker	-5.98 NS	65.8	0.33	-3.11 *	129.3	0.34	1.95 NS	66.1	0.09
S19-90	-8.00 NS	73.6	0.44	-4.92 *	136.7	0.36	3.03 NS	62.3	0.34
S20-20	-8.70 **	76.0	0.76	-5.44 **	137.8	0.75	2.98 NS	62.4	0.30
Sturdy	-6.82 NS	66.6	0.37	-5.52 *	138.3	0.38	-4.13 NS	88.1	0.26

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ R = SCN-resistant.

§ NS = not significant.

Table A-18. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed initial SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, central maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP3035	-14.21 *	100.7	0.64	-3.79 *	144.6	0.36	10.47 *	43.4	0.53
IA2007	-2.37 NS‡	62.8	0.07	-6.40 **	150.6	0.74	-4.08 NS	87.8	0.13
IA2008	-7.75 NS	80.1	0.16	-8.00 **	151.9	0.70	-1.66 NS	76.1	0.01
Jack (R)§	0.08 NS	55.1	0.00	-8.44 *	165.4	0.37	-5.37 NS	96.0	0.44
Kenwood	-5.12 NS	71.0	0.14	-4.31 NS	141.2	0.08	2.39 NS	63.3	0.02
P9272	-6.57 *	69.1	0.52	-3.70 NS	139.5	0.27	-1.28 NS	85.1	0.07
P9273	-3.49 NS	64.5	0.19	-5.20 **	146.3	0.62	-1.47 NS	80.0	0.05
P9381	-0.66 NS	60.0	0.00	-7.25 *	163.2	0.50	-1.78 NS	84.7	0.02
S24-92	-0.65 NS	54.6	0.00	-6.35 *	147.3	0.37	-4.41 NS	87.2	0.35
S28-01	-5.14 *	70.2	0.58	-5.88 **	148.3	0.57	-0.86 *	78.5	0.58

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

Table A-19. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed initial SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, south maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
A92-727017	-3.84 NS‡	73.9	0.33	-8.81 *	170.9	0.48	-1.31 NS	82.5	0.22
C1832	-6.29 **	83.8	0.73	-8.93 **	171.4	0.57	0.09 NS	76.0	0.00
P9303	-18.97 *	124.1	0.59	-9.26 **	165.2	0.51	6.46 NS	51.8	0.41
P9341	-9.09 **	93.3	0.82	-13.14 **	184.8	0.62	-1.14 NS	80.1	0.02
P9381	-7.61 *	87.4	0.69	-11.29 *	177.4	0.33	1.45 NS	69.5	0.04
P9392	-7.98 NS	88.5	0.42	-14.63 *	192.5	0.47	-1.98 NS	85.7	0.37
S30-06	-5.84 NS	81.5	0.11	-7.06 NS	158.8	0.28	-1.59 NS	78.1	0.22
S35-35	-5.48 NS	78.7	0.33	-9.03 *	169.6	0.34	-0.22 NS	78.5	0.00
Sherman	-6.55 NS	84.3	0.28	-9.08 *	166.8	0.35	-3.99 NS	87.8	0.28
Yale (R)§	-8.89 *	91.9	0.63	-10.08 *	176.2	0.34	2.88 NS	67.5	0.27

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

Table A-20. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed mid-season SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, north maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP1989	-7.88 NS‡	73.7	0.19	-2.99 NS	129.9	0.08	3.50 NS	61.0	0.15
AP1993	-10.18 NS	89.6	0.39	-6.22 NS	143.8	0.27	-3.00 NS	80.4	0.21
Bell (R)§	-7.64 **	68.3	0.71	-6.55 *	143.4	0.48	0.07 NS	75.6	0.00
BSR101	-12.89 **	94.2	0.73	-10.23 **	158.6	0.75	3.03 NS	62.1	0.14
IA1004	-3.79 NS	57.7	0.39	-5.72 *	140.3	0.38	-2.55 NS	84.2	0.44
Marcus BC	-5.07 NS	70.5	0.19	-4.04 NS	138.1	0.17	-1.47 NS	77.0	0.30
Parker	-17.69 *	108.5	0.53	-4.92 NS	136.4	0.23	9.87 NS	37.9	0.41
S19-90	-11.12 *	88.1	0.53	-6.66 **	144.3	0.61	3.16 NS	60.5	0.23
S20-20	-20.56 **	122.9	0.65	-5.57 NS	140.6	0.21	10.47 *	34.1	0.58
Sturdy	-4.16 NS	60.3	0.14	-6.11 NS	142.7	0.29	-3.92 NS	89.0	0.24

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

Table A-21. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed mid-season SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, central maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP3035	-23.98 NS‡	141.3	0.47	-5.97 *	153.4	0.38	16.49 NS	18.0	0.33
IA2007	-4.08 NS	70.0	0.11	-6.99 **	154.4	0.65	-3.45 NS	86.5	0.05
IA2008	-4.84 NS	70.6	0.03	-10.70 **	163.4	0.57	-3.92 NS	84.9	0.03
Jack (R)§	-2.73 NS	63.8	0.08	-9.87 NS	165.9	0.20	-4.78 NS	91.4	0.14
Kenwood	-4.96 NS	72.5	0.15	-8.97 **	159.5	0.87	-6.56 NS	97.2	0.19
P9272	-2.49 NS	55.0	0.06	-1.73 NS	132.9	0.04	3.64 NS	66.7	0.46
P9273	-11.47 NS	96.2	0.18	-8.43 **	159.5	0.50	1.76 NS	68.1	0.01
P9381	5.87 NS	35.6	0.11	-8.81 **	170.4	0.54	-9.42 NS	003.7	0.27
S24-92	-13.14 *	100.2	0.61	-8.65 **	155.9	0.69	2.67 NS	62.2	0.06
S28-01	-7.59 NS	80.4	0.39	-5.72 NS	148.6	0.30	-1.26 NS	80.2	0.39

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

Table A-22. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed mid-season SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, south maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
A92-727107	-2.93 NS‡	71.6	0.05	-10.51 **	178.8	0.62	1.08 NS	73.8	0.04
C1832	1.24 NS	55.9	0.00	-12.80 **	185.2	0.57	1.46 NS	70.9	0.06
P9303	-22.76 *	143.2	0.58	-7.49 **	159.9	0.59	7.35 NS	46.8	0.37
P9341	1.62 NS	54.2	0.01	-7.28 *	165.1	0.46	-1.14 NS	80.4	0.01
P9381	2.25 NS	51.9	0.02	-14.06 *	190.2	0.41	3.01 NS	63.1	0.07
P9392	20.77 NS	-16.7	0.24	-16.73 **	201.9	0.72	-2.83 NS	89.3	0.06
S30-06	3.92 NS	44.5	0.02	-5.55 *	155.6	0.36	-0.46 NS	74.2	0.01
S35-35	2.27 NS	51.5	0.01	-7.35 **	167.5	0.52	-2.69 NS	88.4	0.16
Sherman	0.97 NS	56.7	0.00	-7.31 NS	162.9	0.21	0.58 NS	71.2	0.00
Yale (R)§	-8.49 NS	87.8	0.23	-14.45 *	185.5	0.46	-0.57 NS	79.0	0.00

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

Table A-23. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed final SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, north maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP1989	-22.97 NS‡	142.0	0.32	-0.76 NS	122.9	0.01	7.48 NS	41.9	0.13
AP1993	-7.65 NS	85.0	0.21	-3.27 NS	135.2	0.11	-0.36 NS	70.8	0.00
Bell (R)§	-7.37 **	70.8	0.81	-5.40 *	143.1	0.38	0.35 NS	74.7	0.01
BSR101	-5.96 NS	74.8	0.03	-6.73 NS	151.3	0.21	7.84 NS	39.6	0.20
IA1004	-9.55 *	85.2	0.65	-4.23 NS	138.5	0.18	-4.53 NS	94.8	0.36
Marcus BC	-9.68 NS	94.1	0.14	-2.47 NS	134.3	0.04	-3.45 NS	86.7	0.33
Parker	-7.52 NS	79.0	0.08	-2.21 NS	128.6	0.06	3.26 NS	58.4	0.04
S19-90	-47.00 **	245.7	0.87	-12.11 *	171.0	0.50	19.98 **	-12.0	0.84
S20-20	-29.02 **	172.3	0.70	-3.36 NS	134.9	0.10	11.99 NS	20.7	0.41
Sturdy	-12.38 NS	100.0	0.25	-2.33 NS	132.0	0.03	-0.11 NS	76.4	0.00

*, ** significant at the 0.05 and 0.01 probability level, respectively.
† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.
‡ NS = not significant.
§ R = SCN-resistant.

Table A-24. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed final SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, central maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
AP3035	-8.17 NS‡	86.3	0.07	-3.13 NS	144.6	0.26	3.48 NS	65.3	0.02
IA2007	1.08 NS	49.5	0.00	-3.67 NS	143.7	0.25	-3.29 NS	87.7	0.02
IA2008	9.49 NS	11.0	0.09	-7.27 *	154.8	0.44	-4.58 NS	90.1	0.03
Jack (R)§	1.57 NS	50.4	0.03	-1.74 NS	141.5	0.01	-9.73 NS	107.7	0.59
Kenwood	-20.24 NS	145.0	0.31	-4.36 NS	144.8	0.31	25.34 NS	-43.4	0.34
P9272	-14.30 NS	108.6	0.25	-3.11 NS	139.6	0.16	-1.03 NS	85.0	0.00
P9273	-8.59 NS	90.1	0.13	-3.97 NS	145.3	0.18	14.93 *	9.4	0.55
P9381	-19.62 NS	141.0	0.42	-10.30 **	180.3	0.72	19.99 NS	-6.6	0.39
S24-92	-3.27 NS	66.8	0.01	-6.55 *	152.9	0.44	-9.63 NS	114.2	0.21
S28-01	11.21 NS	3.11	0.45	0.86 NS	124.3	0.01	1.87 NS	67.4	0.45

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

Table A-25. Results of linear regression analysis of days after planting to the R1† (DAPR1), R8 (DAPR8), and total reproductive period (TOTALR) versus log_{10}-transformed final SCN population densities (eggs 100^{-1} cm^{-3} soil) for the 1994 field experiment, south maturity set.

	DAPR1			DAPR8			TOTALR		
Genotype	Slope	Y intercept	R^2	Slope	Y intercept	R^2	Slope	Y intercept	R^2
A92-727017	8.48 *	23.4	0.51	-7.98 *	174.5	0.38	-1.40 NS	84.0	0.08
C1832	1.27 NS‡	54.9	0.02	-8.59 *	175.8	0.50	-1.71 NS	83.9	0.36
P9303	-6.21 NS	84.4	0.03	-6.70 NS	161.6	0.26	6.18 NS	47.5	0.18
P9341	6.43 NS	31.9	0.14	-7.72 NS	171.6	0.30	5.75 NS	50.4	0.22
P9381	7.00 NS	30.5	0.17	-12.52 *	189.7	0.46	5.10 NS	52.8	0.16
P9392	8.34 NS	24.8	0.48	-11.06 *	188.2	0.37	-0.39 NS	80.4	0.01
S30-06	11.85 *	7.2	0.65	-2.92 NS	146.9	0.08	2.28 *	62.1	0.64
S35-35	7.10 NS	29.0	0.25	-5.20 NS	162.1	0.27	1.60 NS	70.6	0.11
Sherman	9.12 NS	20.4	0.45	-1.39 NS	141.7	0.01	5.47 NS	49.4	0.45
Yale (R)§	-7.82 *	87.7	0.63	-9.45 *	173.3	0.36	2.89 NS	67.7	0.36

*, ** significant at the 0.05 and 0.01 probability level, respectively.

† R1 and R8 = beginning bloom and harvest maturity, respectively (Fehr et al., 1971); TOTALR = R8 - R1.

‡ NS = not significant.

§ R = SCN-resistant.

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